The

American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

Arthur L. Schipper, *Editor*

CONTENTS

Vol. 55 January, 1956 No. 1

NOTE: THE AMERICAN MIDLAND NATURALIST, published quarterly by the University of Notre Dame, contains a wide selection of papers on botany, paleontology and zoology. Each issue contains 256 pages, two of which comprise a volume.

Subscription rate per year $10.00 in the U. S., Mexico and South American countries; $11.00 elsewhere.

Authors will be requested to pay for tabular material of more than two pages and for engraving costs above $10.00. A subsidy will be required for papers which exceed twenty journal pages in length.

Available issues of Vols. 1-6, 50 cents; Vol. 7, 35 cents; Vols. 7-12, 50 cents; Vols. 13-14, 60 cents; Vol. 15, 75 cents; Vols. 16-18, $1.00; Vols. 19-48, 50, $6.00 a volume, single issues $2.75. Vol. 49 Nos. 1, 3, $2.75 each; Vol. 49 No. 2, $4.00.

Inquiries concerning subscriptions should be addressed to *The American Midland Naturalist*, Notre Dame, Indiana.

Abbreviated citation: *Amer. Midl. Nat.*

The American Midland Naturalist is indexed in the BIOGRAPHY INDEX and the BIBLIOGRAPHIC INDEX.

Entered as second-class matter at Notre Dame, Indiana. Acceptance for mailing at special rate of postage provided for in section 1103; Act of October 3, 1917, authorized on July 3, 1918.

The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

VOL. 55 JANUARY, 1956 No. 1

Studies on the Male Reproductive System of the California Pocket Gopher (Thomomys Bottae Navus Merriam)[1]

W. C. Gunther[2]

Valparaiso University, Valparaiso, Indiana

Investigation of seasonal trends in the activity of the reproductive system of the California pocket gopher has been based mainly on post-mortem examinations of gross structures. Scheffer (1938) reported that the gopher in southern California mates in spring, and that during late spring or early summer the gonads undergo involution until the following spring. Bond (1946) suggested that the breeding activity of the gopher may be related to temperature, amount and time of rainfall, or other factors. Thus, he states that in Orange County, California, breeding activity begins in the latter part of September and ends in the latter part of May, apparently coinciding with the rainy season of this region. Storer (1942) mentioned the possibility that a year-around period of breeding might exist for gophers living in irrigated lands. Miller (1946) gathering data from more than 2000 post-mortem examination records, proposed a similar breeding activity for gophers on cultivated, irrigated fields in the vicinity of Davis, California. These and other reports indicate that the reproductive cycle of the pocket gopher may be extremely variable under different conditions, but little is known of the structural changes in the testes or ovaries and accessory reproductive organs correlated with a change of season and breeding activity.

On the other hand, much progress regarding more detailed information on the seasonal activities of other animals has been made. Oslund (1928) prepared an excellent review of the literature to that time on the seasonal variations in the testes of the vertebrates. Bissonnette and Chapnick (1930), described the changes in the testes of the European starling from November to May. Bissonnette (1935) modified the sexual cycle in male ferrets by increasing periods of exposure to light. Brambell (1935) investigated reproduction in the shrew *Sorex*, Risley (1938) in the musk turtle, Aplington (1942) in the amphibian *Necturus*, Pearson (1944) in the shrew *Blarina*, Wislocki (1949) in the deer, and Pearsons, *et al.* (1952) in the hump-nosed bat. Numerous other researches could be cited but will not be considered here. Asdell (1946) gives a good literature coverage on the subject.

[1] The investigation reported herein has been aided by the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago, and by funds provided by the Department of Zoology, University of California at Davis. Manuscript submitted in partial fulfillment for the degree of Doctor of Philosophy at the University of Chicago.

[2] Present address: Valparaiso University, Valparaiso, Indiana.

Since Miller has suggested that the gopher in the Davis, California, vicinity breeds throughout the year, and since in most cases the wild rodent is a strictly seasonal breeder (Rasmussen, 1917; Shaw, 1926; Wells, 1935; Rowlands, 1936; Jameson, 1950; Howard, 1950; Anthony and Foreman, 1951; Jameson, 1953; see also Asdell for a comprehensive review on reproductive patterns), the problem of differences in pocket gophers becomes one of great interest. Is such continuous breeding in gophers due to overlapping of recent new births that reach reproductive stages before any seasonal factor becomes operative, or does this species actually differ from most wild rodents by carrying on continuous reproduction throughout the year?

Because suitable criteria do not exist for denoting the age of pocket gophers captured from the field, it has seemed important to confine a group of adult animals in the laboratory in order to eliminate the possibility of young animals coming to maturity and reproducing prior to the establishment of some mechanism that might account for a single annual cycle. At the same time one must determine whether laboratory confinement alone exercises a modifying effect upon the reproductive system. This investigation, therefore, utilizes for comparison animals that were captured from the field each month of the year and those sacrificed from the laboratory colony.

Acknowledgments.—The problem was suggested by Prof. Carl R. Moore, Department of Zoology, University of Chicago, and grateful acknowledgment is made for his help (which was always prompt and cheerful although we were separated by more than 2000 miles during the course of the study), especially for his critical reviews of the manuscript.

All animals were captured, maintained, autopsied, and processed at Davis, California. Special thanks are tendered Profs. Lauren E. Rosenberg and Tracy I. Storer, Department of Zoology, University of California at Davis, for their generosity in freely extending use of the facilities and equipment of the department, and for their interest and encouragement.

MATERIALS AND METHODS

The observations presented here were made from studies on a total of 106 male pocket gophers. These animals were captured in an alfalfa field approximately three miles from Davis, California, on the University of California Farm, at an elevation of about 51 feet above sea level. The mean annual rainfall is 17 inches and the mean annual temperature is 60°F. Most of the rain falls between the months of November and April, there being little or no precipitation from May to October, and the fields on the University Farm are irrigated during this dry period. A year-around supply of succulent, green forage is thus available to field animals.

Animals were captured in the Howard live-trap (Howard, 1952), and from two to four were autopsied immediately on capture each month from July, 1952, to June, 1953. Such animals are referred to in this paper as "field animals." A group of 50 males was procured early in July, 1952, during irrigation, when it was possible to pick them up as they emerged from their flooded burrows. These 50 animals were placed in separate cages in the laboratory, and from two to four were autopsied each month. They are referred to here as "laboratory animals."

This laboratory group was originally divided into four categories on the basis of the electric ejaculation test (Moore and Gallagher, 1930) and gross examination of the testes. Half the animals were subjected to the electric ejaculation test and the other half classified according to the size and palpa-

bility of the testes as revealed by manually maneuvering the testes from abdomen to scrotal sac. The four categories assigned were 1) animals that produced a definite ejaculate on stimulation, 2) animals that failed to ejaculate when stimulated, 3) animals with large and firm testes easily maneuvered into scrotal sac, and 4) animals with small and flabby testes not easily maneuvered into scrotal sac. It was intended to sacrifice one animal a month from each of these four categories. However, since during the course of any month one or two animals usually died, it was deemed advisable to sacrifice only the surviving animals from any such group so classified. Consequently, for any month two to four laboratory animals were autopsied together with the same number of field animals.

Both laboratory and field animals were sacrificed at the same time each month for a period of one year, from July, 1952, to June, 1953. Laboratory-confined animals were fed rolled oats, rolled barley, lab chow, and occasionally carrots, and showed essentially no modification in weight from field animals.

Whereas both male and female animals were taken in the traps, with notations on weight, condition of pubic symphysis (open or closed), condition of vagina (open or closed), and pregnancies in the female, the present account will be limited largely to a study of the male system.

At autopsy the animals were anesthesized with ether and killed by bleeding from a pneumothorax puncture. The testes, seminal vesicles, two heretofore unreported structures designated herein tentatively as paired coagulating glands and a single dorsal prostate, the lateral prostates, adrenals, thyroid, and pituitary were weighed on an analytic balance, fixed in Bouin's solution, sectioned at six to eight microns, and stained in Ehrlich's hematoxylin. Presence of spermia was determined by hashing the epididymis in physiological saline and examining the suspension under a microscope. The adrenals, thyroid, and pituitary will be omitted from the present account.

In order to determine the effects of castration and male hormone replacement in the gopher, a group of 22 animals was castrated. The testes were removed through a mid-ventral incision after ether anesthesia. Of these, 12 animals were untreated and sacrificed at periods of 5, 11, 15, 30, 90, 120, and 240 days after castration. Ten other castrates were given subcutaneous injections of testosterone proprionate (Eli Lilly and Co.) as outlined below, beginning 65 days after castration:

2 animals	each injected	for 10 days	with 1	mg	testosterone proprionate	per day
2 animals	each injected	for 20 days	with 1	mg	testosterone proprionate	per day
1 animal	each injected	for 30 days	with 1	mg	testosterone proprionate	per day
1 animal	each injected	for 20 days	with 0.5	mg	testosterone proprionate	per day
2 animals	each injected	for 20 days	with 3.0	mg	testosterone proprionate	per day
2 animals	each injected	for 20 days	with 0.12	ml	sesame oil	per day

In addition to carefully dissected complete reproductive systems from males with large testes and motile spermia in the epididymis, there was prepared for study serial sections of 20 microns of certain portions of the accessory reproductive system in order to trace openings of the ducts. Thirty-nine embryos 4 to 32 mm in length were likewise prepared in order to shed some light on the problem of the nature of the organs in question.

In an effort to determine the presence of enzymes active in forming a copu-

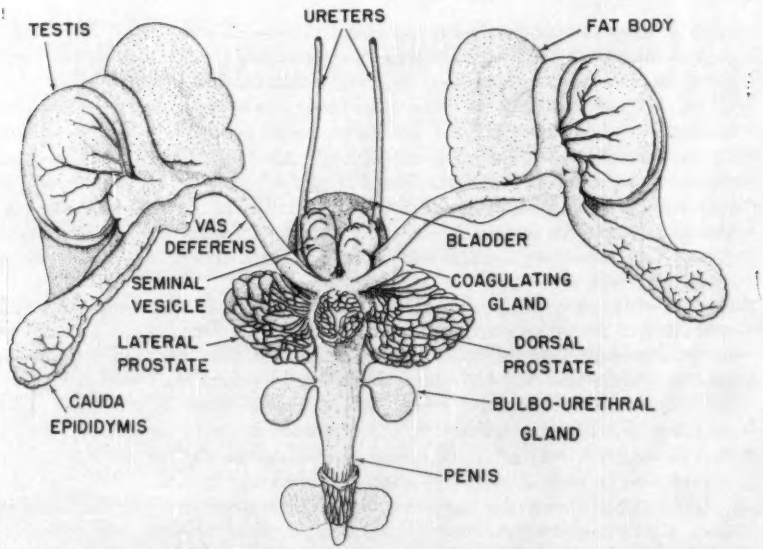


Fig. 1.—Reproductive system of male *Thomomys bottae navus*, dorsal view (×2).

lation plug, the seminal vesicles, coagulating gland, and prostrate of five animals showing motile spermia were removed and treated.

Freshly captured males showed a variation in body weight from 111 to 231 g, and laboratory animals at autopsy showed a similar weight distribution. All weights of internal organs have been converted into milligrams percent of body weight and are so expressed in this paper unless otherwise noted.

OBSERVATIONS

NORMAL MALE REPRODUCTIVE SYSTEM

The gross morphology of the male reproductive system of the pocket gopher has been described in detail by Hill (1937) and requires little additional comment except in the case of the seminal vesicles, coagulating glands, and prostates. The reproductive system of a male with large testes and quantities of epididymal spermia is shown in figure 1.

The seminal vesicle was described by Hill as consisting of a "main, medial, tubular lobe . . . and one (or several) smaller, club-shaped lobes lateral to this." The prostate has been mentioned in the same work as "no specialized coagulating gland as in certain other rodents," and as "a paired structure." As can be seen from a study of figure 1, these descriptions require amplification.

The seminal vesicles of animals with motile spermia consist of a pair of more or less square-shaped structures, with one to several lobules to each gland. The entire organ is quite transparent, and is filled with a sticky, clear fluid. This secretion becomes very hard on fixation, thus causing extreme difficulty in sectioning. Occasionally dispersed in the secretion are round, large, lightly

basophilic masses, non-homogeneous, which appear to be composed of both secretory and cellular elements. These bodies usually lie free in the lumen of a lobule. The lobulation is apparent both externally and internally, but may be seen to best advantage internally in animals without motile spermia. The lumina of each lobe in the gland are irregular and branched, and have numerous outpocketings. In the sexually mature animals the single ducts of these glands can be traced dorsally and caudally for a very short distance to the ductus deferens, where each enters the right or left ductus close to the joining of the latter with the prostatic urethra. In the pocket gopher the seminal vesicles arise as evaginations of the mesonephric ducts, as can be seen in an embryo 31 mm in length, and can be properly homologized with organs of similar origin in other mammals, e.g., man (Watson, 1918) and the rat (Price, 1936).

Hill states that there is no coagulating gland in the gopher. However, the two structures designated as such in figure 1 surely are not a part of the seminal vesicles. The former are two distinct, club-shaped structures, situated medially and slightly dorsally to the seminal vesicles, whose single ducts are parallel and caudal to the vasa deferentia and enter the prostatic urethra as entirely separate structures near, but posterior to, the entrance of the vasa. Usually there is no external evidence of lobulation in this structure, but sometimes one to several lobules appear in cross-section, each surrounded by a thick muscular coat. Only rarely does one find this gland distended and even in this condition, because of the heavy muscularization, it is not transparent. The secretion is clear, but not as sticky as that of the seminal vesicles, and does not harden unduly on fixation. In most instances this structure is in the form of an elongated tube, with numerous projections extending into the lumen from the inner wall. A fairly constant feature of the secreting gland is the presence of small, round, basophilic bodies which are rarely free in the lumen but are usually surrounded by a single layer of cuboidal cells embedded in or surrounded by the secretory epithelium. These are homogeneous structures, unlike those found in the seminal vesicles, and they occur only in the coagulating gland. Bodies of perhaps a similar nature were described by Eadie (1948) in the prostate of a mole. He termed these "amyloid bodies," and suggested that they might function in forming a unique type of copulation plug in the mole. In order to determine whether a similar plug was formed in gophers, the seminal vesicles, coagulating gland, prostate, and bulbo-urethral glands were removed from five males having motile spermia in the epididymis, and each type of gland was hashed separately in physiological saline solution in test tubes. The contents of each tube were then mixed in all possible combinations with the contents of the other test tubes, but no detectable coagulation occurred. This test may not be decisive, however, and should be repeated using animals captured at different seasons. Perhaps the "amyloid bodies" in the gopher function in the manner suggested by Eadie. Evidence for considering this a coagulating gland homologous to those in several other rodents, e.g., the guinea pig (Engle, 1926) and rat (Price, 1936), has been obtained from study of a series of embryos. The coagulating glands in the guinea pig and rat arise from the dorsal portion of the urogenital sinus, ventral to the Müllerian and Wolffian ducts. A structure in this position has been found in a gopher embryo of 31 mm, but immediately earlier or later stages are missing for confirmation. Since some authors (Engle, 1926) consider the coagulating

gland to be a morphological unit of the prostate, and in view of the evidence presented from embryology (comparative histology to be described in the next section), it would not be amiss to consider this structure in the same light and to give it the above name for the sake of convenience. Morphologically it is a constant unit, and in only two cases could it not be found in mature animals. A suspicion is entertained that in these two cases it was so similar to the lobules of the dorsal prostate that it could not be distinguished from them macroscopically.

The description of the prostate given by Hill should be modified slightly regarding position of the lobes. Referring again to figure 1, we see that actually there are two lobes, one on each side of the urethra, with a third lobe situated slightly anterior to the lateral lobes and lying on the dorsal anterior surface of the urethra. In serial sections of the reproductive tract it can be seen that the ducts from each lobe enter the prostatic urethra at their lateral or dorsal positions. Furthermore, from a study of the embryos it is apparent that the lobes arise laterally and dorsally from the urogenital sinus. Therefore, the designation of lateral and dorsal lobes will be used in this report. The middle prostate of the rat (Price, 1936) may be considered homologous to the lateral lobes of the gopher. In moles, however, the ventro-lateral lobes described by Eadie (1947, 1951) are apparently not homologous. The only difference, apart from position, between the lateral and dorsal lobes in pocket gophers appears to be in size, the latter being much the smaller. The prostate, as in most mammals, is a conglomerate of numerous small, compound tubuloalveolar glands. The lumina of the canals and alveoli are very irregular because of the extraordinary folding of the epithelium and because of the numerous diverticula. In distended lobules, however, the lumina become almost perfectly round in cross-section. The secretion is colorless, is not sticky, and does not interfere with sectioning. Round bodies, similar to those found in the seminal vesicles but quite different from those occurring in the coagulating gland, may be found rather rarely in the dorsal prostate and more rarely still in the lateral prostate (possibly prostatic concretions).

SEASONAL VARIATIONS OF TESTES

For a determination of any seasonal trend in testicular activity field animals were sacrificed at the same time each month for an entire year as soon as captured in live-traps. An equal number of laboratory animals was sacrificed with the field animals. The testes were removed, cleaned of fat, and weighed before fixation. The epididymis was finely hashed in physiological saline solution to determine the presence of motile spermia, and sections of the testes were later correlated with their presence or absence. Methods for study of the histology of the testes were divided into several categories. The seminiferous tubule diameter was measured by means of an ocular micrometer. Only those tubules which were perfectly round, or nearly so, were measured, and the average of five such measurements from different sections recorded. The presence or absence of mature spermia in the tubules was noted, as were also the different stages of spermatogenesis. The interstitial cells were measured, and the ratio of nucleus to entire cell was recorded, again as an average of five different cells from different sections. The condition of the cytoplasm and nucleus of these

cells was also noted. The nuclei of the Sertoli cells were measured along one axis only, parallel to the basement membrane, and the position with the average size of five such nuclei recorded.

The testes showed great variability in relative weights of the two testes to total body weight, as well as in the presence of spermia. Body weights of freshly captured males ranged from 111 to 231 g, while those of laboratory animals varied from 111 to 233 g. The raw weights of both testes varied from 0.05 to 3.1 g in field animals, and from 0.08 to 2.3 g in laboratory animals. There was little correlation between testis weight and body weight, largely on account of the activity of the testes. Animals weighing 200 g and more, frequently had testis weights below 1 g, while others weighing less than 200 g occasionally had testis weights heavier than 1 g. As collecting from the field continued it very soon became evident that within the same months some males had testes actively in spermatogenesis with motile epididymal spermia, whereas other males had perhaps large, active testes but no epididymal spermia. Three laboratory males without spermia in the seminiferous tubules had many motile spermia in the epididymis. In the pocket gopher no data exist relative to the length of time spermia may be retained in the epididymis. The size of the animal had little to do with the presence or absence of motile sex cells, for some males with motile spermia weighed as little as 111 g, while others weighing 228 g or more had no epididymal spermia. It is impossible, therefore, to judge sexual maturity or activity on the basis of body weight.

Testis weights (milligrams percent of organ to body weight) for males sacrificed throughout the year are plotted in figure 2 for 38 field and 33 laboratory-confined animals. Such a graph, while showing fluctuations in testis weights from month to month for the population examined, fails to indicate

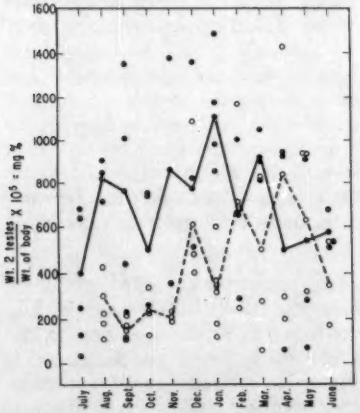


Fig. 2.—Average weight of the two testes in *Thomomys bottae navus* through the year. Field animal individuals = ●, averages = ——; laboratory animals = O, averages = - - - -. (The symbols along the average lines mark monthly points, not individuals.)

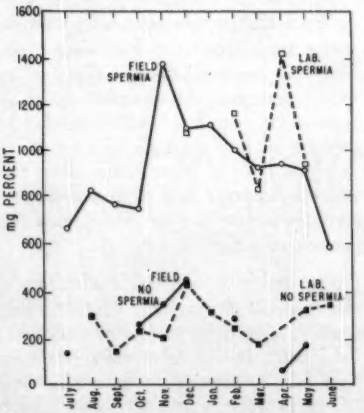


Fig. 3.—Averages of weight of the two testes in laboratory and field animals with and without spermia. (Months with no records indicate no animals taken.)

a distinct seasonal trend in testis activity; it does show that for the two groups testis weights are appreciably lower in laboratory-confined males. The fact that spermia-producing, as well as more inactive, testes are encountered during each month may give false impressions. Another treatment of these data is suggested. In figure 3 testis weights for field males and for laboratory males are plotted on a monthly basis, each group being classified into those with and those without spermia in the testes. Figure 4 gives average testis weights for these same four categories, irrespective of monthly distribution. (The months in which no data are recorded indicate that no animals were autopsied.) These illustrations reveal a few interesting points.

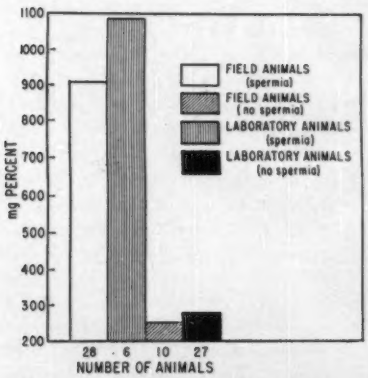


Fig. 4.—Average yearly weight of testes (total weight all testes/number of animals) in the 4 groups of animals.

It can be noted from figure 3 that weights of testes in laboratory-confined males that have spermia in the testes are as great (actually greater, see fig. 4) as the weights of similar testes from field animals. The same holds for testes in which no spermia were present. However, the peak weight of testes from field animals is in November, whereas that from laboratory males does not occur until April. It can be noted further from figure 3 that laboratory males captured in July failed to show complete spermatogenesis until the following December although, as will be brought out below in testis histology, the vast majority of field animals autopsied had motile spermia and complete spermatogenesis during the months of August, September, October, and November. It would have been possible, however, to procure all field animals without spermia for these months (see DISCUSSION). It does appear from these data that laboratory confinement might delay, or even suppress, full testis activity, perhaps as an acclimatization to laboratory conditions, but it does not reduce the actual testis weight during comparable periods of activity.

In order to determine whether laboratory confinement exerted effects on the reproductive system of this wild rodent, the 50 males captured in July were autopsied in groups of two to four each month at the same time as the field animals. If laboratory confinement had no influence on the testes, it would be interesting to determine how long active spermatogenesis was maintained in these animals, and to determine whether any cyclical trend in sexual activity could be discerned. In order to maintain a reasonable control over this aspect, some animals were subjected to the electric ejaculation test immediately on capture. Animals showing motile spermia in the ejaculate were classified as positive, those without spermia as negative. The entire group, however, was not given the test, as it was impossible to obtain consistent results; many animals died, or were hopelessly crippled in the hind quarters. More-

over, while a positive test did indicate the presence of spermia, a negative test did not necessarily indicate the absence of these elements. At best, the ejaculation test affords only a method of approach to the problem. Therefore, 16 of the 50 males were subjected to the test; the remaining were classified on the basis of palpating and manipulating the testes into the scrotal sac. Table 1 brigades the results of this initial classification, and indicates the presence or absence of motile spermia at autopsy. Category 1 indicates animals with a positive ejaculation test showing motile spermia; category 2 indicates animals

TABLE 1.—Classification of laboratory confined animals (see text for interpretation).

Animal No.	Date of autopsy	Presence (+) or absence (—) of spermia in epididymis at autopsy	Categories 1	2	3	4
46	Aug.	—		×		
47	"	+ (no spermia in testes)	×			
65	"	—				×
66	"	—			×	
48	Sept.	—	×			
50	"	—		×		
68	"	—			×	
70	"	— (few dead spermia)				×
49	Oct.	—	×			
88	"	—				×
89	"	—				×
86	Nov.	—				×
90	"	—			×	
69	Dec.	—			×	
74	"	+ (no spermia in testes)				×
51	"	+	×			
53	Jan.	—		×		
60	"	—	×			
72	"	—			×	
75	"	—				×
55	Feb.	—		×		
61	"	+	×			
77	Mar.	—				×
83	"	—				×
67	"	+	×			
56	Apr.	—		×		
71	"	—	×			
79	"	+			×	
76	May	—	×			
59	"	+		×		
80	"	+			×	
62	June	—		×		
84	"	+ (no spermia in testes)				×

that did not yield motile spermia in the ejaculate; category 3 indicates animals with large, firm testes, easily maneuvered into the scrotal sac, and presumably with motile spermia; and category 4 indicates animals with small, flabby testes, not easily maneuvered into the scrotal sac, and presumably having no motile spermia. Checks using extra animals were made on the accuracy of the determination of the conditions under the different categories, but there must be admitted a great deal of subjectivity in categories 3 and 4.

If we keep these reservations in mind, the data show some rather interesting results. Two animals with small, flabby testes at time of capture (category 4), one in December and one in June, had many motile spermia in the epididymis but none in the testes. If, as is presumed, these testes were inactive at the time of capture, then at some time during the year complete spermatogenesis occurred and ceased. The possibility exists for seven other animals in category 4 either to have never had complete spermatogenesis, or to have had complete spermatogenesis at intervals not favorable for showing at autopsy. However, the remaining animal in this category, autopsied in September, must have had complete spermatogenesis prior to this time, for a few dead spermia were seen in the epididymis. None, however, was found in the testes. Five animals with large, firm testes at the time of capture (category 3) had no spermia in the epididymis or testes when autopsied in August, September, November, December, and January. If these animals had spermia at the time of capture, then complete spermatogenesis ceased during the year, and either did not begin again or occurred at short intervals, none of which was detected. Two animals from this group, autopsied in April and May, had motile spermia in the epididymis, and the testes proved to be in complete spermatogenesis. Either spermatogenesis had continued uninterruptedly for a year, or it had occurred at intervals. Six animals with a negative ejaculation test (category 2) had no spermia when autopsied in August, September, January, February, April, and June, but one similar animal autopsied in May had motile spermia. Evidently this latter gopher had testes in complete spermatogenesis at some time during the year. The condition of the testes of the other animals during this interval is not known. One animal in category 1 (positive ejaculation test), autopsied in August, had numerous motile spermia in the epididymis but none in the testes. Complete spermatogenesis had evidently ceased prior to this time. Three other animals in this category had motile spermia in the epididymis at time of autopsy in December, February, and March, while five gophers had no spermia when autopsied in September, October, January, April, and May. These conditions were reflected in the testes. In this group spermatogenesis may have continued uninterruptedly for the three animals with spermia, or it may have been interrupted and resumed at times favorable for showing at autopsy. For the five animals without spermia spermatogenesis may have ceased completely, or it may have ceased and begun at intervals unfavorable for showing at autopsy.

Histological study of the testes was carried out in order to appreciate the variability in their weights. Since the histology of the testes shows decided similarity within those groups of all animals with spermia, and within those groups of all animals without spermia (whether laboratory or field animals), only one representative testis will be described in detail from each group.

In animal no. 170, captured in May with motile spermia in the epididymis,

the testes appeared to be in full activity (fig. 9). The weight of this animal was 153 g, with testis weight 1.4 g. The tubules were open, with mature spermia in many lumina. Average tubule diameter was 306 microns. The interstitial cells were large, with abundant, homogeneous cytoplasm, and the nuclei were round, with peripheral chromatin and a light central part. One to several nucleoli were present. Ratio of nucleus to entire cell was 50%. The Sertoli cells varied considerably in shape and position from one section to another, and were typical of those in the rat (Leblond and Clermont, 1952). The average size of the Sertoli cell nucleus, measured parallel to the basement membrane of the tubule, was 14 microns. The nucleus is often vesiculated and indented, with a very prominent nucleolus. The latter is large, lightly and homogeneously acidophilic, with darker granules around it, sometimes arranged in a manner similar to the spokes in a wheel. Spermatogenesis in this testis, and in others like it, occurs in waves, with a cycle similar to that in the rat. The interest in this testis centers principally on the appearance of the primary spermatocytes. At first glance one would assume that many of the nuclei of these cells are pycnotic and are degenerating. However, the exact appearance of this type of nucleus is retained in all animals whether the testes are showing complete or partial spermatogenesis. With the employment of good cytological techniques perhaps these nuclei could be resolved into a more conformable picture.

In another animal, no. 169, also captured in May (body weight 158 g, testis weight 0.5 g), neither the epididymides nor the testes contained spermia, and sections of the testes revealed the typical inactive condition for these animals (fig. 10). The seminiferous tubules were mostly solid, or with a very small lumen. The average tubule diameter was 153 microns. The interstitial cells were small, with very little cytoplasm, and the nuclei were variously indented, wrinkled, and stained very darkly. Nucleoli were difficult to find. Ratio of nucleus to entire cell size was 80%. The nucleus of the Sertoli cells was generally round, and more often occupied a position toward the lumen of the tubule rather than at or near the basement membrane, and was vesiculated, averaging 12 microns in diameter. Nucleoli were typical. Both nucleoli and vesiculation, and also indentation, are rather constant features of the Sertoli cell nucleus and do not change appreciably under different physiological conditions. Spermatogenesis up to the formation of perhaps secondary spermatocytes was in progress. The maturation of germ cells is usually halted with the formation of spermatocytes in all animals with no spermia.

Table 2 summarizes the histological appearance of the testes in field and laboratory animals with and without spermia. The heaviest testes do not necessarily appear in the heaviest animals, nor do the testes with the least weight appear in the lightest animals. The incidence of complete spermatogenesis is greater in heavier animals, although personal selection may have altered the true picture. As will be explained later, the fact that more field animals with complete spermatogenesis were autopsied may be entirely due to selection. The variability in testis and body weight within each group of gophers is not expressed in the histological picture. Active testes have essentially the same histological appearance, no matter what their weight, and this is true also of inactive testes. Sertoli cell nucleus diameter remains very constant, regardless of season or physiological activity. On the other hand, within each group

TABLE 2.—Summary of testis histology.

Mo.	Animal No.	Body Weight (g)	Testis Weight (g)	Spermia Present or Absent in Epididymis (+ or −)	Tubule Diameter (microns)	Sertoli Cell Nucleus (microns)	Spermatogenesis (Including Presence or Absence of Spermia in Tubules, + or −)	Ratio of Interstitial Cell Nucleus to Total Cell Size (percent)
				Field Animals				
July	41	169	0.05	−	85	10	−; few primary spermatocytes	60
	42	122	0.3	−	170	10	−; many spermatocytes	80
	45	122	0.2	−	153	12	−; many spermatocytes	60
	40	168	1.1	−	289	14	+; all stages	57
	43	209	1.4	+	357	14	+; all stages	57
Aug.	103	202	1.8	+	306	12	+; all stages	45
	104	222	1.6	+	306	10	+; all stages	50
	108	182	1.5	+	272	12	+; all stages	33
Sept.	122	189	1.9	+	255	10	+; all stages	44
	123	208	0.5	+	255	10	+; all stages	44
	124	225	1.0	+	255	12	+; all stages	50
	125	156	2.1	+	272	12	+; all stages	57
Oct.	126	228	0.6	−	187	12	−; many spermatocytes	50
	127	219	1.6	+	306	12	+; all stages	40
	128	209	1.5	+	289	12	+; all stages	57
Nov.	130	147	0.5	−	187	10	−; spermatocytes, occasional spermatids	60
	129	189	2.6	+	289	12	+; all stages	40
Dec.	145	111	0.5	−	170	12	−; many spermatocytes	66
	143	159	1.3	very few	255	12	+; all stages	44
	144	227	3.1	+	340	12	+; all stages	44
Jan.	154	159	2.4	+	272	12	+; all stages	50
	155	231	2.2	+	374	14	+; all stages	40
	156	153	1.8	+	289	14	+; all stages	57
	157	218	1.9	+	340	12	+; all stages	50
Feb.	159	117	0.3	−	187	12	−; many spermatocytes	66
	160	213	2.1	+	323	14	+; all stages	50
Mar.	162	209	2.2	+	272	12	+; all stages	44
	163	199	1.8	+	306	16	+; all stages	57
	164	211	1.7	+	289	14	+; all stages	45
April	167	139	0.08	−	119	12	−; few primary spermatocytes	75
	166	183	1.7	+	323	12	+; all stages	50
	168	165	1.6	+	306	12	+; all stages	50
May	169	158	0.5	−	153	12	−; many spermatocytes	80
	171	178	0.1	−	102	12	−; few primary spermatocytes	75
	170	153	1.4	+	306	14	+; all stages	50
June	174	175	0.9	very few	238	12	+; all stages	50
	175	173	0.9	few	204	12	+; all stages but only few spermia in few tubules	80
	176	211	1.4	+	289	14	+; all stages	66

TABLE 2 (continued).

Mo.	Animal No.	Body Weight (g)	Testis Weight (g)	Spermia Present or Absent in Epididymis (+ or −)	Tubule Diameter (microns)	Sertoli Cell Nucleus (microns)	Spermatogenesis (Including Presence or Absence of Spermia in Tubules, + or −)	Ratio of Interstitial Cell Nucleus to Total Cell Size (percent)
				Laboratory Animals				
Aug.	46	202	0.5	−	238	14	−; many spermatocytes	80
	47	174	0.8	+	255	12	−; spermatogenesis including very few developing spermia, none in tubules	57
	65	172	0.2	−	136	10	−; few primary spermatocytes	75
	66	132	0.2	−	136	10	−; few spermatocytes	75
Sept.	48	162	0.4	−	136	10	−; many spermatocytes	75
	50	229	0.4	−	136	10	−; many spermatocytes	80
	68	186	0.2	−	119	12	−; many spermatocytes	75
	70	227	0.2	− (few dead)	136	10	−; many spermatocytes	75
Oct.	49	186	0.3	−	153	12	−; many spermatocytes	80
	88	186	0.4	−	187	10	−; spermatogenesis including spermatid	57
	89	232	0.8	−	170	12	−; spermatogenesis including spermatid	57
Nov.	86	174	0.3	−	136	10	−; many spermatocytes	80
	90	216	0.5	−	170	10	−; many spermatocytes	60
Dec.	69	233	1.1	−	238	12	−; spermatogenesis including metamorphosing spermatids	50
	74	111	0.5	+ (one live spermium)	153	10	−; many spermatocytes	60
	51	191	2.1	+	323	12	+; all stages	66
Jan.	53	212	0.4	−	204	12	−; many spermatocytes	80
	60	128	0.5	−	170	10	−; many spermatocytes	60
	72	173	1.1	−	204	12	−; spermatogenesis including spermatids	80
	75	151	0.2	−	119	10	−; few primary spermatocytes	75
Feb.	55	175	0.4	−	187	10	−; many spermatocytes	80
	61	193	2.3	+	306	12	+; all stages	50

TABLE 2 (continued).

Mo.	Animal No.	Body Weight (g)	Testis Weight (g)	Spermia Present or Absent in Epididymis (+ or −)	Tubule Diameter (microns)	Sertoli Cell Nucleus (microns)	Spermatogenesis (Including Presence or Absence of Spermia in Tubules, + or −)	Ratio of Interstitial Cell Nucleus to Total Cell Size (percent)
Mar.	77	122	0.08	−	119	10	−; few primary spermatocytes	75
	83	144	0.4	−	170	12	−; few primary spermatocytes	80
	67	203	1.7	+	289	14	+; all stages	57
April	56	209	0.4	−	170	12	−; many spermatocytes	60
	71	139	0.4	−	170	10	−; many spermatocytes	80
	79	159	2.3	+	323	12	+; all stages	50
May	76	130	0.4	−	187	12	−; spermatogenesis with few spermatids	80
	59	215	2.0	+	323	12	+; all stages	50
	80	167	1.6	+	306	12	+; all stages	57
June	62	195	0.3	−	170	12	−; many spermatocytes	80
	84	118	0.6	+	221	12	−; spermatogenesis with few spermatids	80
	177	135	0.2	−	170	12	−; many spermatocytes	75

seminiferous tubule diameter and ratio of interstitial cell nucleus to cell size changes markedly and rather constantly with different activity. Thus, tubule diameter in all animals is wide in active testes (204-374 microns, average 292 microns, in field animals; and 221-323 microns, average 312 microns, in laboratory animals) and narrow in inactive testes (85-187 microns, average 151 microns, in field animals; and 119-255 microns, average 170 microns, in laboratory animals). In general, large testes have large tubules, but size of testes is not directly proportional to tubule diameter. Tubule diameters do not exhibit a cyclical trend.

The ratio of interstitial cell nucleus to complete cell size has proved a constant and reliable criterion of testis activity when correlated with the appearance of these cells. The value of 57% or less of nucleus to interstitial cell size is usually correlated in the active testis with abundant homogeneous cytoplasm, a round or oval nucleus seldom wrinkled or indented, good nucleoli, and rather distinct cell outlines. Ratio values of 60% and higher in the inactive testes are generally associated with a poor and meagre cytoplasm; the cells are packed together, the nucleoli are difficult to distinguish, and the nucleus is seldom round, but very wrinkled, indented, and contorted. When the values of this ratio for the different months are plotted, no seasonal trend is readily apparent, and the variability shown may be explained as being due to technical difficulties in measuring such cells.

Animal no. 177, provided through courtesy of Dr. Walter Howard, Department of Zoology, University of California at Davis, was autopsied in

June, 1953, after approximately 15 months of laboratory confinement. There was essentially no modification from other laboratory animals without spermia. The histological summary in table 2 indicates the same conditions as obtain in other animals of this type.

An outstanding feature of this histological summary is that at least some degree of spermatogenesis is maintained in all of these animals, regardless of the size of the animal, the size of the testes, or the presence or absence of spermia in the tubules. A completely degenerating or involuting germinal epithelium was not found in any of the field or laboratory animals. There appears to be no readily discernible seasonal trend in any of the hsitological features examined in the testes of these gophers.

SEASONAL VARIATIONS OF ACCESSORY REPRODUCTIVE ORGANS

In order to determine any seasonal trend or cyclical activity of the accessory sex structures, the seminal vesicles, coagulating glands, and dorsal and lateral prostates of both laboratory and field animals were removed at the monthly autopsies. Each organ was carefully cleaned of fat and connective tissue, freed from any connection down to the base of its ducts, and separately removed and weighed prior to fixation.

The weights of all secondaries show great variability, very similar in scope to that seen in the testes. There was no correlation in size of the accessories to body weight, nor to the size of the testes. It also was impossible to determine whether an animal had motile spermia simply by observing the gland *in situ*, although usually in field animals the accessory structures are quite distended and sometimes transparent when the testes are active. In general, active testes have complementary large accessory organs, while inactive testes are correlated with secondary structures of a very small size. However, there exists a great discrepancy between the weights of the accessory sex organs in field animals and laboratory animals with spermia, and a lesser difference between the two groups of animals without spermia. The bar graphs in figure 5 summarize this difference. Field animals with spermia invariably have on the yearly average heavier secondary reproductive structures than laboratory animals with spermia, and laboratory animals with no spermia have heavier accessories than field animals with no spermia, except in the case of the dorsal prostate where they are equal. Figure 6 represents an effort to determine in presumably sexually active animals whether, on a monthly basis, secondary reproductive structure weights

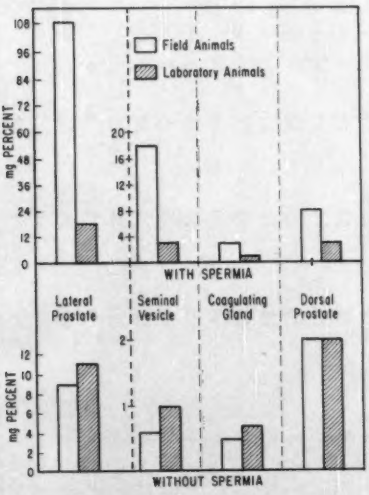


Fig. 5.—Average yearly weight of accessory sex organs in all intact animals.

TABLE 3.—Summary of histology of secondary reproductive structures.

Mo.	Animal No.	Spermia present or absent in tubules of testes (+ or −)	Height of Epithelium (microns)			Amount of Secretion[3]			Secretory Activity[3]		
			SV[4]	CG	LDP	SV	CG	LDP	SV	CG	LDP
						Field Animals					
July	41	−	10	Absent	12	+	Absent	+	0	Absent	0
	42	−	14	Absent	16	0	Absent	0	+	Absent	+
	45	−	20	Absent	10	0	Absent	0	+	Absent	0
	40	+	24	Absent	18	++	Absent	++	++	Absent	++
	43	+	30	Absent	24	+++	Absent	+++	++	Absent	+++
Aug.	103	+	36	34	18	+++	+	+++	+++	+++	+++
	104	+	38	26	28	+++	+	+++	+++	+++	+++
	108	+	26	10	12	++	+	0	+++	0	+
Sept.	122	+	36	18	22	+++	+	+++	+++	+++	+++
	123	+	40	26	18	+++	+	++	+++	+++	+++
	124	+	60	26	18	+++	++	++	+++	+++	+++
	125	+	26	18	18	+++	+	+	+++	+++	+++
Oct.	126	−	12	16	8	0	+	0	0	+	0
	127	+	32	24	20	++	++	++	+++	+++	+++
	128	+	26	26	26	+	+	+++	++	++	++
Nov.	130	−	8	8	8	0	0	0	0	0	0
	129	+	40	26	22	+++	0	++	+++	+++	+++
Dec.	145	−	12	10	12	0	0	0	+	+	+
	143	+	24	22	24	+	0	+	+++	+++	+++

TABLE 3 (continued)

Mo.	Animal No.	Spermia present or absent in tubules of testes (+ or −)	Height of Epithelium (microns)			Amount of Secretion[3]			Secretory Activity[3]		
			SV[4]	CG	LDP	SV	CG	LDP	SV	CG	LDP
						Field Animals					
	144	+	32	20	26	+++	+	++	+++	+++	+++
Jan.	154	+	30	20	22	+++	0	+	++	++	+++
	155	+	36	22	24	++	+	++	+++	+++	+++
	156	+	26	22	22	+++	+	+	+++	+++	+++
	157	+	26	22	22	+++	+++	++	+++	+++	+++
Feb.	159	-	20	24	20	0	+	++	+	+++	+++
	160	+	22	Absent	18	+++	Absent	++	+++	Absent	+++
Mar.	162	+	38	32	24	+++	+	++	+++	+++	+++
	163	+	36	24	22	+++	+	+++	+++	+++	+++
	164	+	30	30	18	+++	+	++	+++	+++	+++
April	167	-	12	20	8	0	0	0	0	+	0
	166	+	26	Absent	20	++	Absent	++	+++	Absent	+++
	168	+	42	26	16	+++	+	++	+++	+++	+++
May	169	-	20	24	24	++	++	++	0	++	+++
	171	-	12	14	10	+	0	0	0	0	0
	170	+	24	20	24	+++	+	+	+++	+++	+++
June	174	+	26	30	22	+++	+	++	+++	+++	+++
	175	+	14	22	26	0	+	+	0	++	++
	176	+	30	18	20	+++	+	++	+++	++	+++

TABLE 3 (continued)

Mo.	Animal No.	Spermia present or absent in tubules of testes (+ or −)	Height of Epithelium (microns)			Amount of Secretion[3]			Secretory Activity[3]		
			SV[4]	CG	LDP	SV	CG	LDP	SV	CG	LDP
						Laboratory Animals					
Aug.	46	−	10	14	10	0	+	+ + +	0	0	0
	47	−	20	28	16	+	+	+	+ +	+	+ +
	65	−	16	16	10	+ +	+	+ +	+ +	0	0
	66	−	10	10	10	+	0	+ + +	0	0	+
Sept.	48	−	10	10	8	0	+	+	0	0	0
	50	−	Absent	16	16	Absent	+	+ + +	Absent	0	0
	68	−	10	16	10	0	0	+ +	0	0	0
	70	−	10	Absent	18	0	Absent	+ +	0	Absent	0
Oct.	49	−	10	12	12	0	+	+ +	0	0	+
	88	−	10	18	10	0	+	0	0	+	0
	89	−	10	10	10	+	0	+	+	+	+
Nov.	86	−	8	10	10	0	+	+	0	0	0
	90	−	14	14	10	+	0	+ +	+ +	+	+
Dec.	69	−	24	12	16	+ +	0	+	+ +	+	+
	74	−	10	10	8	0	0	+	0	0	0
	51	+	10	12	12	0	0	+ + +	+	+	+
Jan.	53	−	10	Absent	10	0	Absent	+	0	Absent	0

TABLE 3 (continued)

Mo.	Animal No.	Spermia present or absent in tubules of testes (+ or -)	Height of Epithelium (microns)			Amount of Secretion[3]			Secretory Activity[3]		
			SV[4]	CG	LDP	SV	CG	LDP	SV	CG	LDP
						Laboratory Animals					
	60	-	8	10	8	0	0	0	0	+	0
	72	-	12	14	6	+	0	+	0	++	0
	75	-	6	6	8	+++	++	++	0	0	0
Feb.	55	-	10	10	10	0	+	0	0	+	0
	61	+	14	20	14	0	+	++	+	+	+
Mar.	77	-	8	20	6	0	+	+	0	0	0
	83	-	10	10	10	0	+	+	0	0	0
	67	+	22	20	16	+++	+	+	+++	++	+++
April	56	-	12	8	8	0	++	++	0	0	0
	71	-	10	12	8	0	0	+++	0	0	0
	79	+	30	Absent	20	+	Absent	++	++	Absent	+
May	76	-	14	16	10	0	+	+	0	+	+
	59	+	14	20	10	+	+++	++	+	+	+
	80	+	16	22	12	0	+	+	++	+	+
June	62	-	10	12	12	0	0	++	0	0	0
	84	-	10	12	8	0	0	++	0	0	0
	177	-	10	10	10	0	0	+	0	0	0

[3] 0 = none; + = meagre; ++ = fair; +++ = abundant.
[4] SV = seminal vesicle; CG = coagulating gland; LDP = lateral and dorsal prostate.

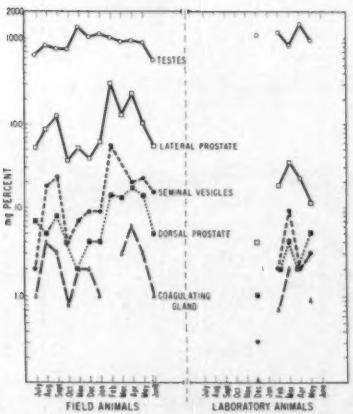


Fig. 6.—Average weight (log scale) of all reproductive structures in laboratory and field animals with spermia.

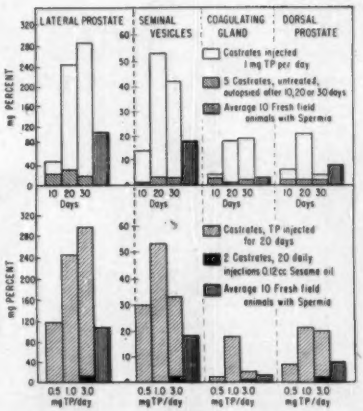


Fig. 7.—Effect of injections of testosterone proprionate on weight of accessory sex organs in castrated animals.

follow the same pattern as testicular weights. It can be readily seen that there is no correlation between the weights of the primary and secondary sexual organs in either laboratory or field animals producing motile spermia. The difference between the average weights of the accessory organs of field and laboratory animals on a monthly basis is noted. There appears to be no seasonal or cyclical trend in these weight distributions.

Similarly, epithelial heights show no seasonal or cyclical trend, and in general accessory organ epithelia are high in animals with spermia and low in animals without spermia. However, the height of the epithelium depends more on the state of secretory activity of the gland than on the condition of the testes. When secretory activity is high, epithelium is high, and the converse is true. It would appear that in a few cases secretory activity is not immediately dependent on the condition of the testes, but in these instances one would be inclined to suspect a testis either coming into complete spermatogenesis or just having completed a full spermatogenetic cycle. In the animals without spermia an increase in the height of the epithelium is almost invariably associated with a small degree of secretory activity, and usually with some quantity of secretion. In animals with spermia, secretory activity can be meagre, fair, or good. For example, animal no. 47, autopsied in August, has a high epithelium in all glands. The amount of secretion is meagre, but the state of secretory activity is fair. Animal no. 46, autopsied in the same month, has a low epithelium in all glands, no secretion in seminal vesicles, a meagre secretion in the coagulating glands, and much secretion in the prostate. Secretory activity, however, is absent in all glands. Table 3 summarizes the histology of the accessory structures.

Seminal vesicles.—Actual weights of the seminal vesicles ranged from 0.1 to 116 mg in field animals and from 0.1 to 19 mg in laboratory animals. In

order to determine how this weight variance affects the histology of the seminal vesicles, studies were made on sections of the glands from all animals. Since glands in a state of high secretory activity are generally similar in their group, and those not exhibiting any such activity are similar in their group, only one gland each from field and laboratory animals with and without spermia will be described in detail. Mention of intermediate stages will be made where appropriate.

In field animal no. 170, captured in June, 1953, whose testes were producing motile spermia, the lobules of the seminal vesicles were distended with secretions. The two glands weighed 34 mg. The simple epithelium in distended lobules is composed of low columnar cells. The round to oval nuclei are varied in position from basal to almost central, although they occupy mostly a basal position, not quite resting on the ill-defined basement membrane. The cytoplasm consists of a homogeneous, slightly granulated substance. Finger-like projections of epithelium extend from the periphery of the lobule into the lumen. The lumen border of the epithelium is very regular, almost as though cut off with a knife, and the amount of cytoplasm in those cells with basal nuclei is about nuclear width. This obviously is in a resting, or at least non-secreting, phase. Usually, however, the lobules are rarely so distended as to lack entirely active secretory epithelium. Where the latter occurs, the epithelium is thrown abruptly into low folds which do not extend any appreciable distance into the lumen, and frequently becomes pseudo-stratified. The lumen border of the epithelium is very irregular, presenting an almost shredded appearance. Nuclei may be seen all the way from the tip of the cell to the basement membrane. The ragged cytoplasm frequently appears to be disconnected entirely from the rest of the cell in a kind of secretion which most closely resembles the apocrine type (fig. 11). The cells in this type of epithelium are probably the actively secreting elements. Large, round bodies occasionally occur in the lumina of the secreting seminal vesicle, and these appear to be composed of aggregates of cellular and secretory elements. Evidently cell destruction is very frequent in these glands. The average height of the epithelium from different portions of the gland where it is feasible to measure is 24 microns.

In the six laboratory animals with spermia, a considerable amount of variation from the typical field condition of animals with spermia is apparent. The average height of the epithelium in these animals is 13 microns, considerably lower than that in field animals with spermia (average, 31 microns). Moreover, this is generally reflected in other histological features. Secretory activity was seldom as pronounced as in field animals, and in some instances quite reduced. The secretion usually found in these glands was entirely absent in three cases, a meagre amount present in two, and typical in only one animal.

In field animal no. 171, with no spermia, whose testes were active only to the production of very few primary spermatocytes, only a meagre secretion was present. This gland weighed 0.5 mg. The epithelium of the lobules was reduced to essentially nuclear diameter; hence, little cytoplasm was present. Frequently the dark nuclei appeared to be in two to several layers, with the lumen layer oblong in section. The other layers of cells occupied more basal positions, and their nuclei were generally round (fig. 12). The lobules appeared collapsed and their lumina very irregular. The average height of the epithelium

was 12 microns. There was no evidence of any secretory activity whatsoever as defined in the preceding paragraph, and the secretion present was probably a storage product of the more active gland. Laboratory animals without spermia have similar epithelia. Intermediate stages in secretory activity are frequent, and the amount of secretion probably constitutes the principal reason for the varying weights in the group of animals with spermia. The same type of epithelium is invariably present in all animals with spermia, but in animals without spermia there are stages present from no secretory activity to a fairly good state, often resembling the appearance of the epithelium in animals with spermia.

Coagulating gland.—The actual weights of the coagulating glands ranged from less than 0.1 to 10 mg in field animals and from 0.1 to 4 mg in laboratory animals.

Unlike the seminal vesicles, this difference in weight appears to be a matter of the development of the secretory features of the gland, rather than an accumulation of its secretion. In the heavier glands lobules are added, each surrounded by a heavy muscular coat. The capabilities for development of these additional lobules may lie resident in the connective tissues between the fibro-muscular layers.

Histological studies were made on sections of the coagulating gland from all animals. Those glands from animals with spermia were very similar in character, and the same applies to animals without spermia. Consequently, only one representative gland from each type of animal will be described in detail.

In field animal no. 170, with motile spermia, the actual weight of the coagulating gland was 5 mg. There was only a meagre secretion present, a condition prevalent in most of the glands studied. Apparently these structures store very little secretion at any time. The epithelium is thrown into deep folds, but none extends completely across the lumen. The folds may be twisted and contorted, and occasionally little islets of tissue are present from these irregularities. Pockets are frequently formed near the edge of the lumen by the overgrowth of the epithelium. Spherical, homogeneous, and slightly basophilic bodies ("amyloid bodies") are present, a condition usually obtained in this gland in animals with motile spermia. These bodies are rarely found in the lumen, and occur in epithelial pockets surrounded by an amazingly regular, single layer of low cuboidal cells. A curious feature of the simple or pseudo-stratified cells of the epithelium is the appearance of the nuclei in the villi projecting into the lumen. In the animal with active spermia the basement membrane extends up into the villus, and the nuclei are oculo-posed[5] (placed in the position or arrangement of buds), and stud the membrane on both sides. The nuclei under such conditions are usually compressed laterally into a narrow leaf-like or, more correctly, drop-like structure, with the small end of the drop attached, or apparently so, to the basement membrane (fig. 13). The manner of secretion is probably apocrine, although very frequently bleb-like formations are seen at the ends of the cells. This epithelium is so characteristic of all animals with spermia, and the secretory blebs and formations so closely

[5] The author is indebted to Prof. J. Clyde Murley, Classics Department, Northwestern University, Evanston, Illinois, for suggesting the term "oculo-posed."

associated with this peculiar type of cell, that there is little doubt that such epithelium is secretory. The nuclei are usually basal, or lower one-third in the cell, but very frequently, particularly when secretory activity is high, may be at the very tip of the lumen end of the cell, or as described above. The average height of the epithelium is 20 microns.

The typical condition of full secretory activity present in field animals with spermia is generally not present in laboratory animals with spermia. The epithelium in the latter averages 18 microns, which is below the average of that measured in field animals (average, 23 microns). The amount of secretion is generally meagre, although stored secretions are rare in this gland for any animals. Secretory activity in laboratory animals with spermia is considerably diminished, as is shown in table 3. In four of the animals with spermia secretory activity was very meagre, and in the remaining animal only fair.

A very different pattern exists in gophers without spermia. Animal no. 171 is typical of the condition in both field and laboratory animals. The coagulating gland weighed 0.5 mg. There was no secretion in this gland, and the basophilic bodies ("amyloid bodies") so characteristic of the secreting gland were absent. The lumen was quite irregular, and the epithelium was folded, projecting at various points towards the center of the gland. No villi with oculo-posed nuclei were present. Any entire cell was hardly wider than its nucleus, which gave the epithelium a very regular appearance, averaging about 14 microns in height. The nuclei were mostly oval in shape, arranged in low cuboidal fashion with their long axis perpendicular to the epithelial surface (fig. 14). No pockets or islets of tissue were discernible. There was no evidence of secretory activity as defined above.

The summary of histology of the coagulating gland in table 3 indicates a maximum in secretory activity in nearly all field animals with spermia. A meagre amount of such activity is present in three animals without spermia, but except in one case is accompanied by a high epithelium. Amount of secretion is generally low in all active glands.

In laboratory animals increases in the height of the epithelium are always accompanied by an increase in secretory activity. Some glands with a low epithelium may have a small amount of secretory activity present. The presence of secretion in the lumina also seems to be independent of secretory activity, showing that there is perhaps some storage in the coagulating gland.

Lateral prostate.—The actual weight of the two lobes of the lateral prostate in field animals ranges from 1.5 to 317 mg, and in laboratory animals from 2 to 70 mg. The increase is accompanied by a tremendous growth in size, primarily due to vast stores of secretion in individual lobules. In order to determine how this weight variation is reflected in the histology of the prostate, studies were made on sections of the gland from all animals. The appearance of these tissues is very similar in all animals with spermia, and the same situation exists among animals without spermia.

In field animal no. 170, whose testes were providing motile spermia, the actual weight of the prostate was 158 mg. Most of the lobules were quite distended with a copious secretion. The epithelium is never flat and compressed as in the seminal vesicles, but numerous villi project into the lumen, some short and some relatively long. The villi in longitudinal section usually consist of

two layers of low columnar cells, with an indistinct basement membrane between. The nuclei of the cells comprising these layers are usually basal. In smaller acini the epithelium becomes more contorted, and typical oculo-posed nuclei seem to hang on a twig of basement membrane within the villi. Associated with this peculiar type of villus are secretory blebs and ragged apical cell cytoplasm (fig. 15). In villi where no secretory activity is evident, the nuclei are basal, oval, and regularly disposed, with apical cytoplasm being about nuclear width in thickness and with lumen edge distinct and well defined. None of the villi appear to be entirely free of such secretory formations, although the smaller, non-distended acini have by far the greater number. The epithelium is similar to that found in the coagulating gland, but no round basophilic bodies ("amyloid bodies") such as are described for the coagulating glands are present. Rounded, slightly basophilic masses occasionally are found lying free within the lumen of a lobule, but these appear to be composed of cellular and secretory elements, quite distinct from the "amyloid bodies." Epithelial height averages 24 microns.

Laboratory animals with spermia do not show as much secretory activity as the field animals, although in kind they are similar. In only one of the laboratory animals with spermia (no. 67) was secretory activity high. Amount of secretion, however , was meagre. In the other five animals secretory activity was meagre, and amount of secretion was usually only fair (table 3).

Animal no. 171, without spermia, had lateral prostates weighing 4 mg. No secretion was evident, the acini were small and numerous, and the lumina very irregular. The villi appear to be entirely absent, and the epithelium is reduced to several layers of cells, containing oval nuclei arranged with their long axis perpendicular to the epithelial surface. The nuclei of the basal layers of cells are round and scattered underneath (fig. 16). The average height of the epithelium is 10 microns. The prostates in field animals with spermia invariably have secretory elements, but those animals without spermia may possess all stages from no acini with secreting cells to several acini with secretion in progress. The prostates in laboratory animals without spermia show a similar picture. The difference in the weight of the prostates in those animals both with and without spermia may be almost entirely due to the amount of secretion present, although a certain amount of growth before secretion may contribute to the size.

Dorsal prostate.—The actual weight of the dorsal prostate in field animals ranges from 0.4 to 44 mg, and in laboratory animals from 0.1 to 11 mg.

The histology of the dorsal prostate will not be described as it corresponds closely to that of the lateral prostate. When the lateral prostate is stimulated the dorsal prostate is likewise stimulated, and the epithelia of both are similar under identical conditions.

The summary of histology in table 3 will serve as a standard for both lateral and dorsal prostates. It usually is the case that epithelial height is increased when secretory activity is high. The converse is also frequently true. Secretion is often present in animals without spermia, and some degree of secretory activity in such animals may be found frequently. Apparently prostatic secretions remain for a much longer period of time than secretions of the other glands.

From this survey of the accessory sex organs it can be seen that great variability exists in the weights and histological features of these glands. There appears to be no correlation among any of the features examined other than generalizations already mentioned. The great difference in weight of the accessories between field animals with spermia and laboratory animals with spermia seems to be not only a matter of lack of secretion and its concomitant secretory activity, but also of retarded development in the latter group. This may be due to the effects of laboratory confinement, although neither the body weights nor the testicular weights of the animals show such effect. Presumably the low epithelium, lack of secretory activity, and low weight are indicative of a low testis hormone secretion in field animals without spermia. What complicates the matter is that in laboratory animals with spermia, in spite of a heavy testis weight and activity equal to that observed in field animals with spermia, the secondary reproductives are lighter in weight and show less secretory activity than the field animals with spermia. In other words, even though all indications are favorable for a normal testis hormone output, either this has been secondarily repressed or the accessories have been rendered more or less insensitive to the hormone by laboratory confinement.

EFFECTS OF CASTRATION

In order to determine the effects of ordinary castration on the secondary reproductive organs of the gopher, and to permit understanding of conditions representing low testis hormonal activity, the testes were removed from 12 freshly captured field animals. These 12 males were castrated in August and were autopsied on days 5, 11, 15, 30, 60, 120, and 240 after castration. One castrate each was autopsied on days 5 and 11, and two each on the other days. At operation the testes in all animals were large, firm, and well vascularized. Examination of the finely hashed epididymis in physiological saline solution revealed the presence of many motile spermia, typical of the condition in field animals with spermia. Presumably, with the testes in this condition, the accessory sex structures showed the same degree of activity already noted in animals of this type, although biopsies were not made at the time of castration.

On the supposition that the weight of accessory organs of each animal at the time of castration was comparable to the weight of similar organs from normal field animals whose testes showed complete spermatogenesis and which were autopsied within a month of the operation on the animals designated as castrates, table 4 gives a comparison of weight loss of the accessories on the

TABLE 4.—Percent of weight loss in accessory sex glands of castrates based on a comparison with normal glands in a high state of activity.

Days after castration	Percent of weight loss after castration			
	Seminal vesicles	Coagulating gland	Lateral prostate	Dorsal prostate
5	76	25	74	43
11	97	25	79	71
15	86	78	72	71
30	86	50	83	71
60	86	75	85	57
120	86	85	83	57
240	90	75	85	43

different days after castration. This presumably suggests a rough evaluation of the rate of involution of these organs upon removal of the testes.

If reliance can be placed upon such a comparison, and the danger in so doing is recognized on account of variability, the table indicates that within five days castration induces a decrease in weight of 76% for seminal vesicles and 74% for the lateral prostate, with a less severe immediate loss in the coagulating glands and dorsal prostate. By the fifteenth day after castration almost all loss in weight of the various accessory glands has occurred, since these losses are quite similar to those found after 240 days. Thus, although reductions in weight have appeared immediately after castration (within five days), there is actually no consistent regression after that time. Rather, it is seen that in some instances increases in weights from a previous low point have occurred. It is unquestionable that removal of the testes causes a drastic involution of the accessories in the gopher when compared with intact animals whose secondary sexual organs are in a high state of secretory activity.

Some further points of interest, and some further complexities of the problem, are introduced by comparisons of the weights (mg %) of accessory organs in castrated males with those from three classes of normal males: 1) intact laboratory-confined males producing spermia, 2) similar laboratory males without spermia, and 3) field animals without spermia. Since marked decline in weights of these organs occurs within five days after castration, and further since 8 of the 12 castrates were autopsied between 30 and 240 days after operation while four were sacrificed from 5 to 15 days, one may assume that average weights represent at least an approximation of complete involution because of removal of male hormone through castration. The comparisons, therefore, should bring out some evidence for the state of hormone secretion by the testes in the three groups of intact males.

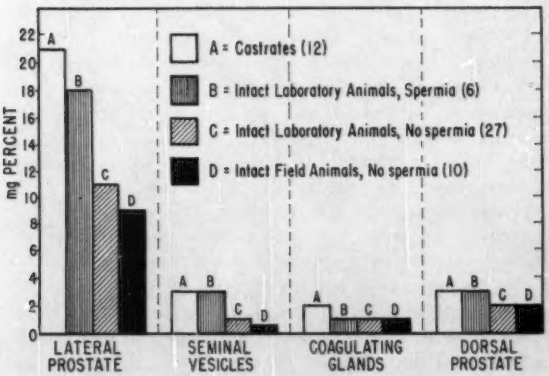


Fig. 8.—Average weight of accessory sex organs in males castrated 5-240 days versus 3 groups of intact males. (Figures indicate numbers of animals in each group.)

Figure 8 presents in the form of bar graphs the results obtained, and reveals unexpected conditions. The average weights of the seminal vesicles in the castrates are the same as those found in laboratory males producing spermia. Similar weight relations hold for the dorsal prostate. In the other two groups of intact males, animals from the laboratory and field with no spermia, the weights of all accessories are actually considerably less than those recovered from the castrate group. In the laboratory animals with spermia, the weights

of the coagulating glands and lateral prostates are also less than those structures in castrated animals.

Several possibilities exist as an explanation of the unexpectedly heavier castrate accessories: 1) Involution may be very slow after castration and the loss of testis hormone is not expressed as a weight loss. The findings in table 4 would not support this explanation, and in the following section it will be shown that the accessory organs increase rapidly in weight upon injection of pure chemical androgens. 2) Other endocrine secretions (pituitary, adrenal, or others) may be responsible in maintaining to some extent the weights of these organs following testis removal. No data presented here bear on that problem. 3) Intact testes at a low spermatogenetic level may produce some substance (e.g., estrogens) that may lead to lower weights of accessory organs.

Histological study of the accessory glands unfortunately adds little of real help in a diagnosis of hormonal secretion. There do not appear to be any consistent definitive morphological characters that would serve to distinguish between castrates and intact animals without spermia. Features such as secretory granules in the seminal vesicle of the rat, or clear areas in the prostate of the same animal, do not appear in the gopher with the techniques employed. Epithelial heights are also not dependable, particularly when comparing castrates with intact males producing no spermia, since the former are frequently the higher. In figure 17 is seen a section of the lateral prostate of a 240-day castrate. The fact that it is impossible to distinguish this from the lateral prostate of an intact, inactive male (fig. 16) is typical of the difficulty encountered when comparing these and other glands of castrates with glands from intact males.

In some of the cells of the epithelia of the seminal vesicles and coagulating glands in a few castrated animals when the cytoplasm is sufficiently abundant, a more or less clear portion occurs above the basal nucleus toward the lumen end. This is not a clear area of cytoplasm, but, rather, involves the entire apical end of the cell. These peculiar cells appear sporadically in the seminal vesicles of castrates of 15, 30, 60, and 240 days, and in the coagulating glands of castrates of 5, 11, 30, and 240 days. None has been noticed in the prostates, and they were not found in any of the glands of intact animals. Since these cells do not appear in all castrated animals, and since they are only randomly scattered in a few portions of the epithelium when they are present at all, they cannot be used as a reliable indicator of the absence of male hormone.

From these considerations it can be deduced that castration, while drastically reducing the weights of the accessories in field animals which have been producing motile spermia, fails to lower these weights to the level of intact field and laboratory animals which are not producing spermia. Likewise, the castrate secondary reproductive structures are maintained at a weight level which is frequently higher than that in laboratory animals whose testes are producing motile spermia. What source, if any, provides the substances necessary to maintain the castrate organs at levels comparable to intact animals is unknown.

EFFECTS OF INJECTION OF MALE HORMONE IN CASTRATED ANIMALS

In an effort to determine how castrated animals respond to treatment with testosterone proprionate, and how sensitive the secondary reproductive struc-

tures are to this substance, 10 gophers with motile spermia in the epididymis were castrated in February, 1953. Eight of these animals were injected with varying amounts of hormone for different periods of time, and two controls were given injections of sesame oil. Comparisons were made also with other untreated castrates, as well as with the average weights from 10 highly active field animals. All animals were castrated 65 days before treatment was begun. Figure 7 summarizes the results of these injections on the basis of milligram percent of organ to body weight. The results must be considered preliminary in nature because of the small number of animals and the inherent variability. Two castrates were treated in each group, except in the case of injections of 1 mg for 30 days and 0.5 mg for 20 days when but a single male in each instance was available.

On the basis of weights of accessory organs daily subcutaneous injections of 1 mg of testosterone proprionate for 10 days, beginning 65 days after castration, led to an appreciable increase in the seminal vesicles and lateral prostate with little or no response of coagulating glands and dorsal prostate. The same daily dose for 20 and 30 days brought all these organs to 100% increase or greater over those from freshly collected field animals in a high secretory state. Twenty daily treatments with 0.5 mg testosterone proprionate led to weights equivalent to accessory organs in normal field animals, while 1.0 and 3.0 mg for similar periods produced much heavier organs. One may therefore conclude that daily treatment with 0.5 mg of this substance produces effects approximately equivalent to those found in intact field males having very active testes. Data from a larger group would probably change this suggested physiological or maintenance dose. Amounts greater than this cause a serious disintegration of the epithelium in all organs, with whole cells in certain areas often cast into the lumen along with the secretion, and even a desquamation of the entire epithelium.

Histological study of the accessory structures reveals that even with the lowest dosage of testosterone proprionate for the shortest period all glands show a maximum of secretory activity. Such activity is expressed not so much in terms of amount of secretion but, rather, in the characteristic type of epithelium with oculo-posed nuclei observed in the highly active glands of field animals. Castrates treated with this androgen have glands that in section are undistinguishable from those of field animals with spermia. Cells with apical clear portions are not found in any of the treated animals. The variability in weight of the glands of the treated castrates appears to be mainly due to the amount of stored secretion.

The glands of the control animals, treated only with sesame oil have the same appearance as the 60-day untreated castrates, including many epithelial cells with the apical clear portions.

From the foregoing it can be deduced that the testes produce a hormone which is responsible for the maintenance of a high state of secretory activity in the secondary sex structures. Removal of the testes causes an involution of the accessories from their active state to a lower level in which secretory activity completely ceases by the end of 60 days. Replacement of the hormone with testosterone proprionate in castrated animals restores secretory activity completely, and increases the weight of the accessories to levels comparable to intact field animals producing spermia.

It can also be inferred that testes in intact field and laboratory animals without spermia are producing a very low quantity of male hormone in some cases and perhaps none at all in others, since there is no consistent difference between the accessories of untreated castrates and these. Judging from the fact that frequently a small amount of secretory activity of the secondary reproductive structures in the above intact animals has been noted, it can be stated that at such times the testes are turning out quantities of hormone, perhaps in prepartion for a complete spermatogenetic cycle.

DISCUSSION

The concept of a fundamental pattern of seasonal breeding activity, especially among wild animals in temperate climates, has been extended by various investigators to include many species. Seasonal breeding is particularly characteristic of the wild rodent, undoubtedly the most numerous member of its class in temperate zones and perhaps the most extensively investigated. This basic pattern appears to have been interrupted in man, domestic animals, some wild animals, and in many common laboratory animals. That a strictly seasonal reproductive pattern is not confined to mammals is readily observable by studying other classes.

Within the Geomyidae reproductive behavior is usually varied. The genus *Thomomys*, as has been noted, has a variable season of breeding activity, apparently due in large measure to the influence of environmental factors. In unirrigated lands the pocket gopher in California appears to have an annual season, coinciding with the period of cool, wet weather in winter and spring. Dr. Walter E. Howard,[6] gathering data over a period of years at the San Joaquin Experimental Range, suggests a single annual cycle commencing and ending in spring for a closely allied sub-species (*Thomomys bottae mewa*) in this natural environment, approximately 150 miles south of Davis, California. In the gopher under investigation as reported in this paper, the influence of a habitat in irrigated fields may be responsible for a drastic shift from the fundamental pattern.

It has been suggested that the inclusion of data from animals both with and without spermia on a non-comparative basis may have little significance in determining any trend in seasonal activity. This is particularly true when considering field animals because of a certain amount of selection of animals on the part of the investigator. Animals captured and autopsied fresh from the field could have included both producers and non-producers of motile spermia during every month of the year. In any month it was necessary to continue trapping until the desired number and type of animal were captured. For example, if three laboratory animals were to be autopsied for any particular month, the same number of field animals was desired. During this period perhaps six field animals without motile spermia were initially captured. Trapping was continued until several animals with spermia were procured. Then, on a purely arbitrary basis, perhaps two field animals with spermia and one without spermia were selected and autopsied. The procedure was varied, with as much consideration as possible being given to body weight values, and during any month it would have been quite possible to secure all animals with

[6] Personal communication.

spermia, or all animals without spermia. Consequently, in field animals, the fact that during one month only animals with spermia were autopsied, while in the next month half the animals had motile spermia and the other half none, was due entirely to the vicissitudes of collecting and had no bearing on the proportion of the two types available from the field. It is doubtful, therefore, that such trends as may appear when grouping the two types are valid, since such data include artificially selected animals both with and without spermia.

In the case of the laboratory animals, initial selection was based on the desirability of placing representative animals into the several different categories mentioned. While four groups were deemed necessary, what was actually wanted amounted to a group of animals with spermia, and a group of animals without spermia, and the categories achieved roughly approximate this objective. Selection of these animals for monthly autopsy was based solely on the surviving number of members from each group. Because of the poor scrotal development and the fact that these animals apparently have the ability to retract their testes into the abdomen at the slightest provocation, it was impossible to judge whether the testes were producing spermia in the live gopher. A very few animals had prominent scrotal testes when brought into the laboratory, but invariably the testes were withdrawn into the abdomen in a few days or less and did not reappear. All animals were kept under constant observation while in the laboratory. The animals whose testes had motile spermia in the epididymis when autopsied almost invariably showed no outward signs as are usually associated with this condition.

In the freshly captured field animals scrotal testes were frequently encountered, and these always had motile spermia. Equally frequently, however, animals which showed no such outward signs possessed testes producing motile spermia. Apparently position of the testes at time of capture or autopsy in no way indicates the breeding condition of the male pocket gopher. That such animals are fecund is suggested by the fact that impregnated females were captured during all months of the year.

Regarding actual reproduction, Miller (1946) has stated that pregnant females were collected in every month of the year, and in my much smaller total number of animals I have personally collected pregnant females in all months during the period from July, 1952, to June, 1953. It therefore becomes apparent that for the wild population females litter throughout the year.

In ordinary, seasonally-breeding animals the beginning of the breeding season in the male is marked by an increase in the size of the testes, followed by an increase in the size of the secondary reproductive structures. During the period of mating the testes produce vast quantities of spermia, and the other organs are maintained at a high level. At the end of the season is noted a gradual decline in size of all organs, which eventually return to their former inactive condition for the duration of the inactive season. During this period of inactivity spermatogenesis ceases entirely and the testes undergo an almost complete regression, with no indication of mitotic figures. This process has been accurately traced in many animals by weighing the testes and secondary reproductive structures, by measuring the height of the epithelium in accessory glands, and by comparing the tubule diameters of active and inactive testes. On a lesser scale histological studies on the various organs have been made in

order to correlate the appearance of tissues with the increase in their weight and with the increase in height of the secretory epithelium. Similar methods were adopted here to determine the seasonality of the reproductive structures in the gopher.

It has been demonstrated in this investigation that the basic pattern described above is entirely lacking in the pocket gopher. Active testes, producing spermia, have been found in field animals during every month of the year, with a correlated activity of the secondary reproductive structures. Inactive testes have also been found in field animals, with a corresponding inactivity of the secondary reproductive structures. The variations noted in all the structures and features examined in field animals suggest, rather than a seasonal variation of the entire group of animals, a cyclical behavior in the individual animal without a necessarily parallel behavior at the same time in other animals. It is proposed that each animal, under its own inherent rhythm, has periods of sexual activity and inactivity. During the periods of activity the testes grow in size, complete spermatogenesis occurs, and the secondary reproductives grow in size and increase in secretory activity. After an unknown period of time, during which the animal discharges its sex products once or many times, a period of regression sets in during which the gopher's sexual structures return to an inactive condition, again for an unknown length of time. This is essentially the pattern in animals with a seasonal reproductive activity. That such a process is possible in the gopher, occurring frequently during the year, is indicated by the indisputable fact that spermatogenesis had never ceased completely in any animals examined, but was carried through at least to the formation of spermatocytes in gophers without motile spermia. All that is necessary to carry the process to completion during any period of activity is the necessary stimulus. Possibly it may be compared to the spermatogenetic waves occurring within the active testes, but on a lesser scale. The sequence of events could be such as to occur in rhythmic fashion in two steps: the first, a sustained activity of the testes at puberty to the formation of spermatocytes; the second, further periodic activitation to complete spermatogenesis. This kind of cyclical activity would be intermediate between the fundamental pattern of strictly seasonal reproduction on the one hand and continuous reproduction at the onset of sexual maturity on the other hand.

The evidence in favor of this hypothesis seems abundant. In a negative sense, the absence of any definite seasonal trends as indicated by weights and epithelial heights precludes the possibility of a mass seasonal sexual activity. The fact that animals have been found possessing motile spermia, or lacking them, regardless of body weight, with considerable overlap in any weight group would indicate in a positive sense (if body weight be a criterion of age) that spermatogenesis is not dependent on an animal reaching a certain weight classification (age) after which spermia are produced continuously for the life of the individual. In a negative sense, this same argument could be used to rule out the possibility that overlapping age groups come into activity before any seasonal factors become operative, since in that event it must be postulated that these animals become sexually mature at the same age (weight), and there is no evidence to support this. If, as research seems to favor, the interstitial cells of the testes produce the hormone which acts upon the secondary reproductive structures, the activity of these elements also supports the hypothe-

sis of alternating cyclical behavior of the sexual organs. In field animals with spermia the ratio of nucleus to total cell size is usually low, and secretory activity of the secondary sex structures usually high. However, whether a testis is producing spermia or not, if the interstitial cell ratio is low some degree of secretory activity in the accessories can usually be discerned. On the other hand, if the ratio is high, whether spermia are being produced or not, secretory activity is usually suppressed. This suggests a function of the interstitial cells to supply the hormone acting upon the secondary reproductive structures. This of itself is not evidence for the theory, but behavior of the interstitial cells supports the view that the cyclical phenomenon under consideration is not seasonal but intermittent in nature, because of the inconstancy of these elements in different animals.

Perhaps the strongest support for the hypothesis of intermittent cyclic waves of sexual behavior in individuals comes from the results of the investigations on the laboratory animals. If we refer to table 1, for the purpose of the present discussion, the animals may be placed in but two categories, those with and those without spermia, at the time they were confined in laboratory cages. Five out of 16 animals classified as animals with spermia were found to have complete spermatogenesis at the time of autopsy. One out of 17 animals classified as being without spermia was also found to have complete spermatogenesis at time of autopsy. Three of the latter group had spermia in the epididymis, but none was found in their testes, and one of the former group had spermia in the epididymis but none in the testes. If an animal had no spermia at the time it was brought into the laboratory, but had active spermatogenesis at the time of autopsy, evidently a complete spermatogenetic cycle must have occurred at some time during the course of its confinement. Contrariwise, if an animal had spermia at the time it was placed in the laboratory, and these had disappeared at time of autopsy, complete spermatogenesis must have ceased during its confinement. It can be stated that, of the two groups mentioned, roughly 40% of those classified as animals with spermia at time of confinement and 25% of those classified as animals without spermia at time of confinement showed positive evidence of spermatogenetic activity during the course of their laboratory life. Furthermore, if secretory activity of the secondary reproductive structures be considered as evidence of either an impending spermatogenetic activity or such activity just completed, it can be inferred from a study of table 3 that an additional four animals with no spermia and nine animals with spermia possibly had complete spermatogenesis during the course of laboratory confinement. Consequently, 21 of the entire laboratory population of 33 animals showed evidence of complete spermatogenetic activity during the course of their confinement, and eight animals from this group of 21 were originally classified as having no spermia. The implication here, then, is that cycles of sexual activity in individuals occurred among this laboratory population at varying intervals.

Allanson (1934), in describing seasonal variation in the reproductive system of the male hedgehog, proposed a breeding season from April to August, and stated that spermatogenesis, at least to the formation of spermatocytes, never completely ceased in the adult animal. Hill (1939) discusses a similar phenomenon in the male weasel. Thus, even in some strictly seasonal

breeders, complete cessation of spermatogenesis does not occur, but it is only partially repressed for periods long enough to indicate a seasonal trend.

In 1917 Rasmussen investigated seasonal changes of the interstitial cells in the testes of the woodchuck, although not relating their function to maintenance of secondary reproductive structures. He described the transition of these elements from poorly developed and few in number to well developed and very numerous upon emergence of the woodchuck from hibernation in spring. According to Rasmussen, the increase in size and number of the interstitial cells was so dramatic as to force the tubules apart and double the diameter of the testes. He further ascertained that spermatogenesis in the testes began while the animal was in hibernation, and that free spermia were present in late March, two or three weeks before the animal awoke. The interstitial cells continued their development and probable increase in number until the last of April, when the testes suddenly underwent a period of spermatogenetic regression. A new spermatogenetic cycle began early in May, and the interstitial cells remained in their complete state of development for at least two months longer. By August the interstitial tissue was reduced to almost naked nuclei. Here is a situation very similar in kind to that seen in the gopher as far as spermatogenesis is concerned. Two waves of spermia formation in the woodchuck followed each other in rapid succession with a complete cessation at the end of the seasonal cycle. In the gopher these successive waves apparently are never interrupted long enough to give a seasonal effect, nor do they occur in all animals at the same time intervals.

How these cycles, their frequency and duration, can be determined in the living animal remains an open question. Mating the males would be a positive procedure, but pocket gophers have not been bred in captivity. When a male and female are placed together in a cage a struggle immediately ensues, usually resulting in the death of the weaker animal. The electric ejaculation test has not proved a constantly reliable source of information. A chemical ejaculation test has been described by Loewe (1937), but has not been attempted here. A rather drastic but perhaps most promising procedure would be to perform biopsies on the testes at varying intervals of time. It is certain that observations made by the customary manipulation, or observation of outward signs, have not proved at all reliable.

Evidence has accumulated from a number of sources that the interstitial cells of the testes are the source of the male hormone responsible for the maintenance of normal secretory activity in the secondary reproductive structures (Moore, 1924; Blount, 1929; Moore and Gallagher, 1930; Greep, *et al.*, 1939; Pollock, 1942; Hooker, 1944; Pearson, *et al.*, 1952). There is no seasonal change associated with the appearance of these cells in the pocket gopher, but there is considerable variation, both in the appearance of the nucleus and in the amount of cytoplasm in the entire cell. This fluctuation appears as a cyclical phenomenon only in that in general it follows the cycles of sexual activity in individual gophers as described above. When the animal's testes are producing spermia, the interstitial cell nucleus is round to oval and smooth, and cytoplasm is abundant. When no spermia are being produced, the nucleus is in a sense polymorphic, often indented, and frequently wrinkled, with a very meagre cytoplasm. These characteristics are often more closely associated with the spermatogenetic activity of the testes than they are with the secretory activ-

ity of the secondary reproductive organs, but usually in the latter case there is a positive correlation also. The inconsistencies may be explained by the methods used to determine secretory activity in the accessory structures, which are at best subjective in the absence of any one constant morphological criterion. In those cases where the ratio of interstitial cell nucleus to cytoplasm is high (poor nucleus, little cytoplasm) and where secretory activity of the accessory organs has been noted, such activity is always very slight and may be interpreted as either the beginning or the end of a cycle. In all cases where the ratio of interstitial cell nucleus to cytoplasm is low (good nucleus, much cytoplasm), secretory activity is pronounced in the secondary reproductive structures. It may be inferred from this that the interstitial cells play a role in the maintenance of secretory activity in the accessory sex organs of the pocket gopher.

In all gophers the Sertoli cells are rather constant elements whose nuclei do not change to any appreciable extent under different physiological conditions. The appearance of the entire cell, including its nucleus, seems to be based on the elements adjacent to it. Where the testes show only partial spermatogenesis the Sertoli cells are scattered rather freely among the spermatocytes and spermatogonia, and the nuclei are rounded structures but still retain their inherent characteristic features. Where complete spermatogenesis occurs, the nuclei are crowded toward the basement membrane and assume a varied shape, depending on the mechanical pressures applied to them by the surrounding germ cells, and the highly developed cytoplasm receives the developing spermia between the active germ cells.

Seminiferous tubule diameter in the testes is directly related to spermatogenetic activity. Where activity of the germ cells includes only development into spermatocytes, the tubule diameter is small, and the lumina are often partially or completely occluded. When activity of the testes occurs beyond spermatocyte formation, the tubules widen in diameter, large lumina appear, interstitial spaces become prominent, and the testes grow in size. Intergrades between these two extremes are found in different animals. Seasonal activity is not discernible, and the diameter differences follow the cyclic variation of the spermatogenetic activity of the testes.

The accessory sex organs are stimulated to secretion simultaneously as a unit in all normal animals, but to a lesser degree in normal laboratory stocks. Secretory activity in this latter group rarely approaches the maximum condition observed in field animals. This accounts in a large measure for the lesser size, in laboratory animals with spermia, of the secondary reproductive structures with their lower average epithelial height. If any influence is exerted by confinement in the laboratory, this would appear to be the only one. Various factors may account for this, factors such as diet, activity, and exposure to other environmental conditions not met in the field. These could operate to depress the quantity of male hormone, or to condition the accessories against making their normal response to androgens. On the other hand, the individual sexual cycles may be of such duration that the secondary structures did not have sufficient time to make a maximum response, or they may have been in the period of regression from such a condition. The variations in weight of accessories within their respective groups may be due partially to an inherent difference in their size.

A condition exists in the case of castrated gophers, consideration of which must be approached with all due caution. The secondary reproductive structures in many animals invariably undergo a drastic involution after castration but can be restored by injections with androgens (Baker, 1927; Moore and Gallagher, 1930; Moore, Hughes, and Gallagher, 1930; Moore, Price, and Gallagher, 1930; Moore, *et al.*, 1934; Wells, 1935; Callow and Deansley, 1935; Zuckerman and Parkes, 1938; Sayles, 1942; see also Moore, 1937, for review). The involution of the accessories in a castrated, seasonally-breeding animal, such as the ground squirrel, is referred to by Wells as being more drastic than in the normal animal at its greatest point of seasonal involution. He, therefore, considers testes in an involuted condition to be turning out minute quantities of androgens sufficient to maintain the accessories at a higher level than is shown in the castrated animal. In the gopher, however, an entirely different situation exists. Castrated males have accessories which are equal to or heavier than those of intact field and laboratory animals with no spermia, and those of laboratory animals producing spermia. It is often impossible to distinguish a castrated from a normal animal without spermia by an examination of the tissues of the secondary reproductive structures, and even the weights of these organs give no clue. As in other animals investigated, testosterone injections restore secretory activity, and weights of organs and the state of the secretory epithelium are rapidly returned to normal in 65-day castrated gophers by such treatment. Consequently, at least in animals with spermia, it would appear that the hormone responsible for the secretory activity of the accessories is resident within the testes. But if minute quantities of hormone are elaborated by the involuted testes, and such secretion maintains a certain influence on the accessories of intact animals, then there ought to be a deviation in castrated animals from the normal condition, a further retrogression. Since this has not been demonstrated in the castrated gopher, further inquiry into the nature of the agent responsible for this condition is required. There is no compensatory hypertrophy of non-secreting elements in the accessories following castration. Secretion already present persists for some time, but there is no indication that this condition is any different from that seen in intact animals. It may be that the secondary structures are maintained at a certain minimal level without the aid of hormones, and that after a certain threshold is reached, following specific androgen stimulation, the structures respond. Or, as has been frequently suggested, sources of the male hormone other than the testes are available and are utilized to maintain a minimal standard of development of accessory structures in all gophers. In the latter case the testes would act to inhibit this production, and when the inhibiting influence is removed the accessories would respond to a slightly greater extent. In this connection a cursory preliminary investigation of material on hand reveals that the adrenal glands of the castrates average slightly heavier on a milligram percent of organ to body weight basis than do these glands in all laboratory and field animals, while the weight of the pituitary averages exactly the same in castrated and normal animals. This may be significant. Moore (1953), however, fails to find any influence of the adrenals on secondary sexual structures in normal rats. If the structures are maintained by an agent other than a hormone, there should be no increase in weight upon removal of the testes unless the testes were inhibiting this influence also. Finally, it may be postulated that the accessory sex organs in the

gopher require a period of greater duration than 240 days in order to reach a state of maximal involution in the castrate.

There is no evidence and therefore no reason for postulating a hormonal control of testes and accessory organs essentially different from that already proposed by Moore and his colleagues. The pituitary, under the influence of certain intrinsic factors, is stimulated at puberty to release a minute quantity of gonadotrophin into the blood stream, which directly affects the testes and which, in the pocket gopher, presumably maintains a minimal amount of spermatogenetic activity at all times. Under certain conditions (perhaps extrinsic factors such as environment, diet, etc., or even such an intrinsic factor as an inherent rhythm within the animal itself) the pituitary is stimulated to secrete more of the gonadotrophin, and spermatogenesis is pushed through to completion. An interesting speculation in this regard is that possibly the secretion of the gonadotrophin remains at a constant low rate, and bursts of periodic complete spermatogenetic activity are initiated by response of the testes to a certain threshold level achieved through "summation" effects. If this latter were true, it might account for the fact that the pituitary in castrated animals shows no increase in weight over normal animals, since the body might be able to dispose of this minute quantity through other channels and no "storage" would result in the pituitary; or else it might take a longer period of time for storage products to accumulate and be recognized. In either case the secondary reproductive structures would respond in normal animals to the increased activity of the testes. In the former case, the greatly increased production of androgens by the active testes would have an inhibitory action on the pituitary, depressing the amount of secretion of gonadotrophins, and the testes, with this stimulus removed, would be returned to their partially involuted state, with a concomitant reduction of secretory activity in the accessories. If the testes respond to "summation" effects, the androgen, of course, would have little direct effect on the pituitary at any time. Before this concept can be extended, however, response of the normal animal to gonadotrophins should be determined, and also the potency of the pituitary of castrated as compared with normal animals should be investigated. Work on the other seasonally-breeding animals so far indicates that the testes respond to gonadotrophins at any time of the year, that the pituitary of the castrated animal has a greater gonadotrophic effect than that of normal animals, and finally that the pituitary of sexually inactive males is generally less potent than that of males taken during the breeding season. An assay of the pituitary, taken from members of similar groups of field and laboratory animals under investigation in this paper, should yield interesting results.

SUMMARY

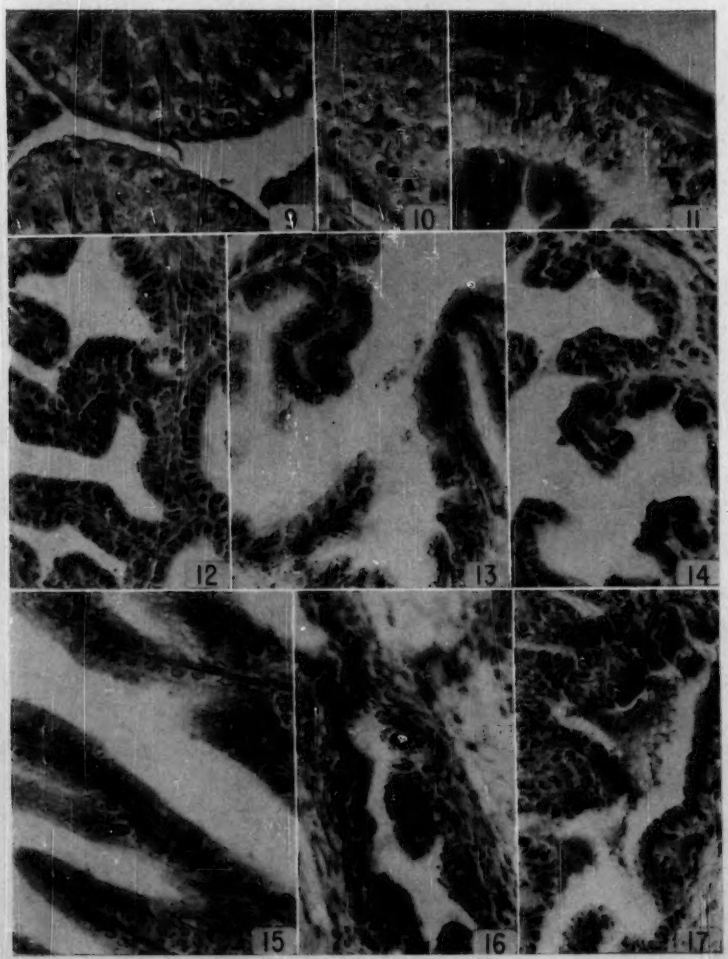
Studies on the male reproductive system of the California pocket gopher in the vicinity of Davis, California, based on laboratory and field populations autopsied at monthly intervals for a period of a year, have been described.

Two structures, a coagulating gland and dorsal prostate, hitherto unreported, have been proposed as constant elements of the male gopher's reproductive system. Homologies of these and other portions of the reproductive system have been discussed.

A type of cyclical reproductive activity has been suggested for the gopher, neither seasonal nor continuous, but intermediate in scope, during which indi-

vidual animals undergo alternating periods of sexual activity and partial testicular regression without regard to season or age once maturity has been attained. Spermatogenesis and other testicular functions have been discussed.

The histology of the accessory sexual organs in the normal animal has been



Figs. 9-17.—9. Testis tubules in active spermatogenesis; 10. Testis tubule showing partial spermatogenesis; 11. Actively secreting epithelium, seminal vesicle; 12. Inactive epithelium, seminal vesicle; 13. Actively secreting epithelium, coagulating gland; note oculo-posed nuclei bottom and top left; 14. Inactive epithelium, coagulating gland; 15. Actively secreting epithelium with oculo-posed nuclei, prostate gland; 16. Inactive epithelium, prostate gland; 17. Epithelium, prostate gland, 240-day castrate. (All figs. ×275)

described. Characteristic round, homogeneous bodies in the active coagulating gland, and an unusual type of secretory epithelium in all accessory organs studied, have been included in the descriptions.

Castration results in a rapid reduction in size of all accessory reproductive organs, and treatment with chemical androgens rapidly restores weight losses and epithelial appearance. However, both intact field and laboratory males without complete spermatogenesis and laboratory males with spermia may possess secondary sex structures of smaller size than males castrated for 240 days. Further study is required to resolve several peculiarities in the exceptional reproduction of this wild rodent.

REFERENCES

ALLANSON, M. 1934—Seasonal variation in the reproductive organs of the male hedgehog. Phil. Trans. Roy. Soc. B 223:277-303.

ANTHONY, ADAM AND DARHL FOREMAN 1951—Observations on the reproductive cycle of the black-tailed prairie dog (*Cynomys ludovicianus*). Physiol. Zool. 24(3): 242-248.

APLINGTON, H. W. 1942—Correlative cyclical changes in the hypophysis and gonads of *Necturus maculosus* Rafinesque. I. The male. Amer. J. Anat. 70:201-244.

ASDELL, S. A. 1946—Patterns of mammalian reproduction. Comstock Publishing Co., Inc., Ithaca, N. Y.

BAKER, J. R. 1927-28—Influence of age at castration on the size of various organs. Brit. J. Exp. Biol. 5:187-195.

BISSONNETTE, T. H. 1935—Modification of mammalian sexual cycle. III. Reversal of the cycle in male ferrets (*Putorius vulgaris*) by increasing periods of exposure to light between October 2 and March 30. J. Exp. Zool. 71:341-373.

——— AND MORTON HERMAN CHAPNICK 1930—Studies on the sexual cycle in birds. II. The normal progressive changes in the testis from November to May in the European starling (*Sturnus vulgaris*), an introduced, non-migratory bird. Amer. J. Anat. 45:307-344.

BLOUNT, R. F. 1929—Seasonal cycles of the interstitial cells in the testis of the horned toad (*Phrynosoma solare*). J. Morph. and Physiol. 48:317-343.

BOND, R. M. 1946—The breeding habits of *Thomomys bottae* in Orange County, California. J. Mamm. 27:172-174.

BRAMBELL, F. W. ROGERS 1935—Reproduction in the common shrew (*Sorex araneus* Linnaeus). Phil. Trans. Roy. Soc. B 225:1-62.

CALLOW, R. K. AND R. DEANSLEY 1935—Effect of androsterone and of male hormone concentrates on the accessory reproductive organs of castrated rats, mice and guinea pigs. Biochem. J. 29:1424-1445.

EADIE, W. ROBERT 1947—The accessory reproductive glands of *Parascalops* with notes on homologies. Anat. Rec. 97:239-252.

——— 1948—The male accessory reproductive glands of *Condylura* with notes on a unique prostatic secretion. Ibid. 101:59-80.

——— 1951—A comparative study of the male accessory genital glands of *Neurotrichus*. J. Mamm. 32:36-43.

ENGLE, EARL T. 1926—The copulation plug and the accessory genital glands of mammals. Ibid. 7:119-126.

GREEP, R. O., F. L. HISAW AND H. L. FEVOLD 1939—A testis stimulating extract of brewer's yeast. Anat. Rec. 73:297-306.

HILL, JOHN E. 1937—Morphology of the pocket gopher mammalian genus *Thomomys*. Univ. Calif. Publ. Zool. 42:81-172.

HILL, M. 1939—Reproductive cycle of the male weasel (*Mustela nivalis*). Proc. Zool. Soc. B 109:481-512.

HOOKER, C. W. 1944—The postnatal history and function of the interstitial cells of the bull. Amer. J. Anat. 74:1-37.

HOWARD, WALTER E. 1950—Winter fecundity of caged male white-footed mice in Michigan. J. Mamm. 31:319-321.

——— 1952—A live trap for pocket gophers. Ibid. 33:61-65.

JAMESON, JR., E. W. 1950—Determining fecundity in male small mammals. Ibid. 31:433-436.

——— 1953—Reproduction of deer mice (*Peromyscus maniculatus* and *P. boylei*) in the Sierra Nevada, California. Ibid. 34:44-58.

LEBLOND, C. P. AND Y. CLERMONT 1952—*in* Biology of the testes. Ann. N. Y. Acad. Sci. 55(4):543-742.

LOEWE, S. 1937—A pharmacological ejaculation test for bio-assay of male sex hormone. Proc. Soc. Exp. Biol. Med. 37:483-486.

MILLER, MILTON A. 1946—Reproductive rates and cycles in the pocket gopher. J. Mamm. 27:335-358.

MOORE, CARL R. 1924—Properties of the gonads as controllers of somatic and psychical characteristics. VI. Testicular reactions in experimental cryptorchidism. Amer. J. Anat. 34:269-316.

——— 1937—Testis hormone secretion and some effects of the hormone in the organism. Cold Spring Harbor Symposia on Quantitative Biology 5:115-122.

——— 1953—Adrenal cortical secretions in relation to the reproductive system of rats. J. Cl. End. and Met. 13:330-368.

——— AND T. F. GALLAGHER 1930—Seminal vesicle and prostate function as a testis-hormone indicator; the electric ejaculation test. Amer. J. Anat. 45:39-69.

———, WINIFRED HUGHES AND T. F. GALLAGHER 1930—Rat seminal vesicle cytology as a testis-hormone indicator and the prevention of castration changes by testis-extract injection. Ibid. 45:109-136.

———, DOROTHY PRICE AND T. F. GALLAGHER 1930—Rat prostate cytology as a testis-hormone indicator and the prevention of castration changes by testis-extract injection. Ibid. 45:71-108.

———, GEO. FINLAY SIMMONS, L. J. WELLS, M. ZALESKY AND WARREN O. NELSON 1934—On the control of reproductive activity in an annual-breeding mammal (*Citellus tridecemlineatus*). Anat. Rec. 60:279-289.

OSLUND, R. 1928—Seasonal variations in testes of vertebrates. Quart. Rev. Biol. 3:254-270.

PEARSON, OLIVER P. 1944—Reproduction in the shrew (*Blarina brevicauda* Say). Amer. J. Anat. 75:39-94.

———, MARY R. KOFORD AND ANITA K. PEARSON 1952—Reproduction of the hum-nosed bat (*Corynorhinus rafinesquei*) in California. J. Mamm. 33:273-320.

POLLOCK, W. F. 1942—Histochemical studies of the interstitial cells of the testis. Anat. Rec. 84:23-29.

PRICE, DOROTHY 1936—Normal development of the prostate and seminal vesicles of the rat with a study of experimental postnatal modifications. Amer. J. Anat. 60:79-127.

RASMUSSEN, A. T. 1917—Seasonal changes in the interstitial cells of the testis in the *Marmota monax*. Ibid. 22:475-515.

RISLEY, P. L. 1938—Seasonal changes in the testis of the musk turtle, *Sternotherus odoratus*. J. Morph. 63:301-318.

ROWLANDS, I. W. 1936—Reproduction of the bank vole (*Evotomys glareolus* Schreber). II. Seasonal changes in the reproductive organs of the male. Phil. Trans. Roy. Soc. B 226:99-120.

SAYLES, E. D. 1942—The effects of castration upon the reproductive organs of the adult male guinea pig. J. Exp. Zool. 90:183-197.

SCHEFFER, T. H. 1938—Breeding records of Pacific coast pocket gophers. J. Mamm. 19:220-224.

SHAW, WILLIAM T. 1926—A short season and its effect upon the preparation for reproduction by the Columbian ground squirrel. Ecology 7:136-139.

STORER, TRACY I. 1942—Control of injurious rodents in California. Calif. Agr. Ext. Serv. Circ. 79.

WATSON, E. M. 1918—The development of the seminal vesicles of man. Amer. J. Anat. 24:395-442.

WELLS, L. J. 1935—Seasonal sexual rhythms and its experimental modification in the male of the thirteen-lined ground squirrel (*Citellus tridecemlineatus*). Anat. Rec. 62:409-447.

WISLOCKI, G. B. 1949—Seasonal changes in the testis, epididymides and seminal vesicles of deer investigated by histochemical methods. Endocrinology 44:167-189.

ZUCKERMAN, S. AND A. S. PARKES 1938—The effects of male hormone on a mature castrated Rhesus monkey. Jour. Anat. 72:277-279.

Variation in the Fox Squirrel in Florida[1]

Joseph Curtis Moore
American Museum of Natural History, New York, N. Y.

The form of fox squirrel which occupies western and central Florida has for many years borne the name *Sciurus niger niger*. It has shared this name with fox squirrels which inhabit the sunny, open pine forests of the coastal plain northward to southeastern Virginia (Handley and Patton, 1947) and westward into southeastern Alabama (Howell, 1921). Its several color phases caused early confusion and has made it a somewhat difficult species with which to work.

The form restricted to the southwestern tip of peninsular Florida first received recognition from Howell (1919), who described it from a single specimen from Everglades, Collier County. This form, *Sciurus niger avicennia*, has since been reported by Hamilton (1941) on the basis of two sight records, at Fort Myers and Tice, Lee County. Bailey (1930) making no mention of specimens or specific observations, reported it "east and west" of Paradise Key, which is a bit of high land in the Everglades National Park about 12 miles southwest of Homestead, Dade County, and also in the pine

Fig. 1.—*Sciurus niger avicennia* at Everglades, Florida, Dec. 28, 1953. Side view, feeding. Photograph by Ralph S. Palmer.

[1] Portion of dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Florida, January, 1953.

and cypress fingers reaching toward the mangrove in Collier and Monroe counties. Christy (1928) reported seeing one, ". . . in the mangrove forest near Cape Sable. . . ." Moore (1954) reported their occurrence as town squirrels in the little city of Everglades and their known occurrence in the Everglades National Park. As far as published records go, it appears that only one specimen of *Sciurus niger avicennia* has been described.

Fox squirrel material from northern and middle Florida, Howell (1919) found, did not quite agree with a series, ". . . from southern South Carolina—the type region of *Sciurus niger*." and ". . . the coast region of Georgia (Barrington and Hursman's Lake)." He commented that in the Florida material the common or gray color phase differs by being, ". . . darker above and tinged with buff below." He also noted that the buff phase was more numerous in the available series of Florida skins.

Considerably more material has become available since 1919. An attempt is made in the present study to define the geographic ranges of races of fox squirrels occupying western, central, and southern Florida, and to present detailed descriptions of the color phases exhibited, and a statement of the proportion in which these phases occur. The amount of available material being greatest for the race occupying central Florida, data on individual variation in this form is presented for color of the pelage and characters of the skull.

Acknowledgments.—I am indebted to H. B. Sherman of the Department of Biology, University of Florida, for support, encouragement, suggestions and criticism. W. C. Allee, head of the same department, contributed helpful criticism and guidance in the preparation of the manuscript. B. B. Leavitt of the same department contributed also by helpful criticisms and encouragement. Ralph S. Palmer visited the type locality of *S. n. avicennia* with me and obtained a beautiful series of photographs, one of which has been used in this paper (fig. 1). The Graduate School of the University of Florida granted tenure of the Dudley Beaumont Memorial Fellowship during the fall of 1949 when this work was begun. The interest of superintendent Daniel B. Beard of the Everglades National Park has been an important source of help. E. Ross Allen of Silver Springs noticed a difference between the fox squirrels of western and of central Florida and drew it to my attention as early as 1946. When this study had been in progress for some months, word reached me that F. S. Barkalow, Jr., of the University of North Carolina had begun work earlier on a revision of the fox squirrels of the Atlantic coastal plain. It developed that he had not yet begun work on Florida material and he graciously agreed to a division of our study at the Florida State line. Richard Davis generously helped me with the statistics involved in table 3. The help of these and many others is gratefully acknowledged.

The following persons and institutions lent fox squirrel skins and skulls for use in this study. They are listed in the order of amount of material lent. The initial will be used in text references to show location of material. (Specimen numbers preceded by an M refer to the author's collection.)

MCZ—Museum of Comparative Zoology, Harvard University
USFWS—Biological Surveys Collections, U. S. Fish and Wildlife Service
USNM—United States National Museum
ANSP—Academy of Natural Sciences of Philadelphia
AMNH—American Museum of Natural History, New York
JAW—Priv. coll. Jay A. Weber, Miami
CMNH—Chicago Museum of Natural History
DBUF—Department of Biology, University of Florida
CAS—The Chicago Academy of Sciences
MVZ—Museum of Vertebrate Zoology, University of Wisconsin
HBS—Priv. coll. H. B. Sherman, Deland, Florida

CM—Carnegie Museum, Pittsburgh, Pennsylvania
RMAG—The Reading Museum and Art Gallery, Reading, Pennsylvania
MZUM—Museum of Zoology, University of Michigan
AS—Priv. coll. Albert Schwartz, Charleston, S.C.
MNUK—Museum of Natural History, University of Kansas
MZLS—Museum of Zoology, Louisiana State University
BAB—Priv. coll. B. Austin Barrington, Bristol, Tennessee
SLB—Priv. coll. Stephen L. Beckwith, Gainesville
PGP—Priv. coll. Paul G. Pearson, New Brunswick, N.J.
GHP—Priv. coll. George H. Pournelle, San Diego, California

The writer is very grateful to the authorities of these institutions and to the owners of these private collections for their courtesy and for the opportunity to examine this material.

METHODS

MEASUREMENTS

So much difference is apparent in body measurements made by different collectors that use of such measurements in this study is largely avoided. Skull measurements, which can be made in consistent manner by one person, are more generally employed here. The following series of skull characters were measured on each skull where possible. (Specimens apparently collected with shotguns often had sustained damage which rendered some measurements impossible. Some specimens had had the gnathion cut away during the skinning or fleshing of the skull and could not provide measurements requiring its use.)

Condylobasal length.—Greatest distance from the anterior surface of the gnathion to the posterior surface of the right occipital condyle.

Palatal length.—Distance between the foremost point of the gnathion and the foremost point on the posterior margin of the palate.

Diastema.—Distance from the most anterior point on the right upper premolar to the posterior surface of the right upper incisor just ventral to the alveolus.

Candylo-premolar length.—Greatest distance from posterior surface of right occipital condyle to anterior surface of right upper premolar.

Maxillary tooth-row.—Greatest distance between anterior surface of right upper premolar and posterior surface of right upper third molar.

Dentary cheek-tooth row.—Greatest distance between anterior surface of right lower premolar and posterior surface of right lower third molar.

Interorbital width.—Least distance between mesial notches in orbits.

Span of post-orbital processes.—Greatest distance from tip to tip.

Zygomatic breadth.—Greatest distance between outer surfaces of zygomata in a transverse plane which transects the masticatory foramina (Hill, 1935).

Post-orbital constriction.—Least width of skull in this constriction.

Mastoid breadth.—Greatest distance between outer surfaces of mastoid processes.

Palatal breadth including teeth.—Greatest distance between labial surfaces of maxillary tooth-rows.

Palatal width between premolars.—Least distance between lingual surfaces of upper premolars.

Width of upper premolar.—Greatest distance between lingual and labial surfaces of right upper premolar.

Width of lower premolar.—Greatest distance between lingual and labial surfaces of right lower premolar.

Rostral depth.—Least distance from anterior edge of incisive foramina to dorsal midline of rostrum.

Occipital depth.—Least distance from intersection of the lambda suture and mid-dorsal line to a line connecting the most ventral point of each occipital condyle.

Measurements were also taken of rostral width, palatal width between premolars, least distance between temporal ridges, upper incisor length, and zygoma depth. These, however, proved uncertain measurements or of no use in the present work. A vernier caliper with parallel jaws was used exclusively in making these measurements.

COLOR DESCRIPTION

Audubon and Bachman (1851, p. 133, pl. 68) describe three color phases of *Sciurus niger* and provide a color plate showing two of these and another about which there is some doubt. These authors mention (p. 134) that the nose and ears are white in all color phases of this race. The phases they describe are: 1) A *gray phase* with white feet and belly, agouti back, and tail hairs white excepting for the black band. 2) A *black phase* which is black all over excepting for the white nose and ears and a few white hairs on the feet and in the tail. 3) A *black-bellied phase* in which head thighs, and belly are black, and the back and tail "dark gray" (undoubtedly agouti). They add that there is a fourth variety, but both the geographical occurrence and description they give for it indicate that it represents a separate race to which Lowery and Davis (1942) give the name *Sciurus niger bachmani.* Audubon's color plate mentioned above faithfully depicts color phases 2 and 3. The third animal on this plate agrees with the fourth phase description given by Audubon and Bachman, and excepting for the white toes insisted upon by Lowery and Davis, with the description of *Sciurus niger bachmani.* It seems more reasonable to presume that it depicts this animal which Audubon and Bachman have discussed than a buffy phase of *Sciurus niger niger* which they have not described.

With the advantage of specimens accumulated during the 68 years after the Audubon and Bachman account, Howell (1919, p. 37) states

> Typical *Sciurus niger* is subject to great variation in color and exhibits three well-marked phases. These may be called the gray phase, the buff phase, and the black or melanistic phase. The gray phase in its extreme form (specimen from Georgetown, S. C. . . .) is pale gray above, including the tail, and white beneath. The crown is black or blackish and the nose, ears, and feet are white. Some specimens in this phase have the feet and under side of the tail buff, thus approaching the next darker phase. In the buff phase the general tone of the upper parts is pinkish buff, the underparts, feet, and underside of tail rich cinnamon-buff or clay color. Numerous intermediate specimens connect this phase with the gray phase. The black or melanistic phase . . . is wholly or partly black or dark brown, except the nose and ears which are white.

There is a tendency in the above, and by more recent authors delineating color phases in this species, to select the palest gray individual, the blackest, and the buffest, and to describe them as the "well-marked" phases and all other individuals as "intermediate." If applied to the population sample from central Florida where these extremes are rare, this view-point would relegate the great majority of individuals to the rather anomalous category of inter-

mediates. A large number of intermediates is inevitable in the fox squirrel population of central Florida, but it is possible in the present study to describe phases which are consistent color patterns noticeably characterizing a portion of the population.

The extreme variability of Florida fox squirrels in pelage color led me to avoid the multitude of tints and shades which use of Ridgway's (1912) color standards would have involved, and to lump the colors observed under ten names. Certain specimens were used as standards for comparison until the writer felt that these were well enough established in his mind for him to proceed without the standards before him.

The pelage phenomena recorded as "colors" for the purposes of this study were white, whitish, pale tan, tan, pale buff, buff, pale agouti, agouti, blackish agouti, and black. In actual use of these colors in the present study pale tan has not been distinguished from tan, nor pale buff from buff, nor pale agouti from agouti; hence from here on the terms tan, buff, and agouti include their diluted forms. White needs no explanation, but whitish includes approaches to white such as extremely pale agouti and that of pelage which is probably white but dirty. Tan includes all the warm pelage colors whose brilliance was too high to show (by my concept) any trace of red, and too infused with yellow or brown to show any pink. Buff includes all of the pinks and reds, and hues between red and yellow and brown of brilliance lower than those included in tan. In Ridgway (1912) my definition of tan includes Maize Yellow, Baryta Yellow, Pale Yellow Orange, Buff Yellow, Cartridge Buff, Ivory Yellow, Cream Buff, Deep Colonial Buff, Pinkish Buff, Light Buff, Warm Buff, and Pale Ochraceous Buff. My definition of buff in the fox squirrels includes Ridgway's (*op. cit.*) Pale Yellow Orange, Capucine Buff, Orange Buff, Light Orange Yellow, Capucine Orange, Capucine Yellow, Chamois, Honey Yellow, Olive Ocher, Pale Pinkish Buff, Pinkish Cinnamon, Light Pinkish Cinnamon, Cinnamon, Light Vinaceous Cinnamon, Vinaceous Cinnamon, Clay Color, Orange Cinnamon, Cinnamon Buff, Vinaceous Tawny, Onion-Skin Pink, Buff Pink, Pale Ochraceous Buff, Light Ochraceous Buff, Ochraceous Buff, Ochraceous Orange, Antimony Yellow, Light Ochraceous Salmon, Ochraceous Salmon, Zinc Orange, Apricot Buff, and Salmon Color. The designations agouti, and blackish agouti refer only to the extent that the hairs are black-banded or black-banded and black. Infusion of other color in agouti areas is ignored. Black includes an occasional pelage which is a dark brown or reddish black. Harper (1927) describes a specimen from the Okefinokee Swamp which had a molt line separating the shining black fresh pelage of the anterior half of the body from the worn, blackish brown to auburn pelage of the posterior half. A molt line around the middle of a black specimen of *Sciurus niger avicennia* examined by the writer also separated old reddish-black fur from new, shiny black fur. Reddish black or brownish black fur in all the Florida fox squirrel material studied by the writer is considered to be old, worn, black fur and is tabulated as black.

For each skin a pelage color description was separately recorded, for nineteen areas of the pelage listed in table 4. For partial skins as many of these color data as could be obtained were recorded. The claws were consistently blackish with translucent tips throughout this material and will not be further discussed.

More than one color was sometimes present on one pelage area. This was recorded and for most pelage areas all of the colors are used in the tabulated comparisons (resulting in total percentages exceeding 100 in tables 2, 4). The exceptions to this are tips of tail hairs, basal bands of tail hairs, and venter. In the first two of these, deviation from one color is characteristically that of paling distally along the length of the tail, and only the proximal, stronger color is used. Color of the venter characteristically pales in the axils of the limbs of both sexes and around teats of parous females. This paler color is not included in the tables. The pelage color of the front legs, nape, back, and sides, was usually agouti. Although other color occurred on the non-black portions of the agouti hairs, varying from strong buff to whitish, only the agouti for these specific pelage areas is here-in discussed. The hind legs above the foot agree so consistently with the sides laterally and with the venter mesially that they are not regarded as separate pelage areas.

Some authors have referred to the color of the ventral side of the tail as different from that of the dorsal side. This is only apparently true. Excepting for the tendency to be paler toward the distal end of the tail, all hairs on the tail are ordinarily colored alike. Each hair has a long basal band of white, tan, or buff, next a band of black, then a tip of white, tan, or buff. The thatched arrangement of the hairs on the dorsal surface of the tail conceals the usually more intense color of the basal bands of the hairs, excepting when the hairs are erected in excitement of some kind. On the ventral surface of the tail, however, the hair arrangement is distichous, coming out only from the sides with no ventral hairs present to form a concealing thatch. The more intensely pigmented basal bands of the hairs show, therefore, in a ventral view of the tail. The black band occurs on all of the tail hairs excepting in places where the tail has been injured and hairs which are entirely white grow out from the injury, and in some cases in which the tail appears to be white-tipped through heredity rather than injury.

CRITERIA FOR SELECTION OF COMPARATIVE MATERIAL

It was possible in the present study to distinguish parous from non-parous females by the teats, usually even in dried skins, parous ones having nipples about 3 mm long and non-parous ones about 0.5 mm. No secondary sex character proved so satisfactory for sorting out adult males. Allan (1942) suggested for fresh males the use of size and pigmentation of the scrotum, but admitted that this distinction was not satisfactory. The parous condition of females as determined by length of the teats is not a sufficiently inclusive criterion of adulthood because it not only excludes males from consideration but some females which appear to be fully adult and which have nevertheless not borne young. However, it does appear to be an excellent criterion for the individuals to which it applies, and hence provides a standard by which other criteria may be selected.

Presence of fully erupted permanent premolars and evidence of toothwear were used by Setzer (1949) as criteria of adulthood in study of the kangaroo rat, and are considered here. Permanent and deciduous upper premolars are distinguishable in Florida material by the greater linguo-labial breadth of the former and the occlusal triangularity of the latter. For central Florida speci-

mens a linguolabial breadth of 3.1 mm or more for the upper premolar correctly separates 142 of the 149 specimens with permanent premolars, and breadth of 2.7 mm or less distinguishes 16 of the 27 specimens with deciduous premolars. The remainder were easily distinguished by shape, which appears to be an entirely constant character. Since the difference in shape is only safely learned by examining series including both kinds, the breadth measurement is of value in distinguishing permanent or deciduous premolars in small series, or as an aid in learning to distinguish the shapes. In figure 2 comparison of the

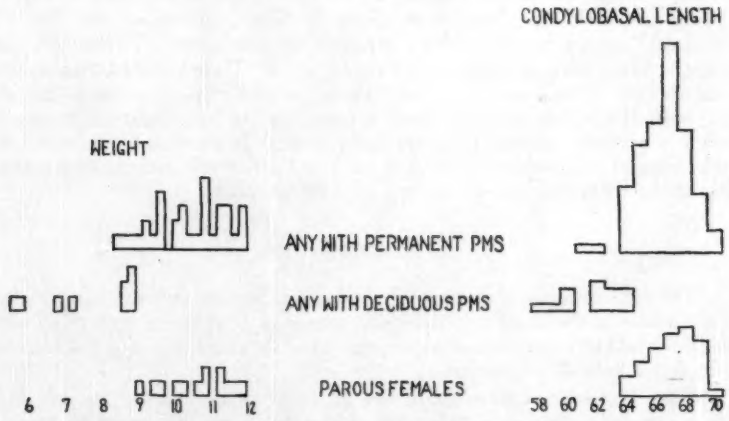


Fig. 2.—Comparison of the parous female fox squirrels of central Florida with all individuals of that area having fully erupted permanent premolars, and with those not having such. Comparison is in millimeters of condylobasal length and hectograms of weight.

parous females with all individuals having fully erupted permanent premolars, and those not having such, shows that presence of fully erupted permanent premolars may be used as a rough criterion of adulthood and full growth.

In an effort to assign relative ages to the specimens studied, the writer classified all skulls examined in this study on a tooth eruption and tooth wear scale of ten categories:

1. No cheek-teeth erupted.
2. Some but not all cheek-teeth erupted.
3. All cheek-teeth erupted, but enamel not worn through on any cusps.
4. Enamel worn through on some lower cusps, but no upper.
5. Enamel worn through on some upper and lower cusps, but not worn through on transverse ridge of upper M3 to expose gray dentine all the way across.
6. Enamel of transverse ridge of upper M3 worn through all of its length, but ridge not reduced to lowest level of occlusal surface of tooth.
7. Ridge so reduced, but at least one cusp remaining on upper premolars.
8. All cusps worn away, but roots of lower M3 not visible through occlusal surface.
9. Roots of at least lower M3 but not all molars visible through occlusal surfaces.
10. Roots of all upper molars visible through occlusal surfaces.

TABLE 1.—Toothwear classes of parous and non-parous female central Florida fox squirrels.

	Classes									
	1	2	3	4	5	6	7	8	9	10
parous			3	3	19	16	9	5		
non-parous			6	7			1			

To evaluate use of this toothwear scale as a means for sorting out adults in the Florida fox squirrel material, the toothwear classes of parous and non-parous central Florida females are shown in table 1. Here we find that 49 of the 55 parous females (89%) are in class 5 or above. Thirteen of the fourteen non-parous females are in classes 3 and 4. There is a 14th non-parous one which is in toothwear class 7 and which has skull characters clearly indicating mature size, but this individual is considered to be a fully adult animal which for reasons unknown has not borne young. It therefore appears that in this material toothwear classification of 5 or higher will exclude immatures, but at the expense of also excluding 12.5% of the adults.

SEXUAL DIMORPHISM

The twin histograms of figure 3 show no differences between adult males and females of the whole central Florida sample in 17 different skull characters which would warrant separation of the sexes in examining this population sample for individual variation.

Table 2 provides a color comparison in the 19 pelage areas of 78 male and 95 female fox squirrel skins from central Florida. Some differences are apparent in small portions of the sample, but no color character distinguishes the sexes in a part of the sample large enough to justify examining the sexes separately for individual variation.

INDIVIDUAL VARIATION

SKULL CHARACTERS

Interest in which measurable skull characters might be the most stable within a subspecies and hence probably be better characters for use in comparing that subspecies with some other, led the writer to study the individual variation in 16 skull characters. For this the most abundant material proved to be from central Florida. Table 3 shows individual variation in a series of 93 skulls, which included all of the available skulls from central Florida with a toothwear classification of 5 or higher. The coefficients of variation indicate that width of upper premolar is the most stable of the 16 characters. This was, furthermore, the only character of which it was possible to obtain a satisfactory measurement in 100% of this material. These two facts enhance the value of the use of this character for a criterion of maturation mentioned above. This and width of lower premolar are of small dimension, however. Of larger characters the condylo-premolar length stands out as most stable. Palatal length appears to be the least variable of the more traditionally used characters.

Palatal breadth including teeth is an innovation of considerable stability in this sample.

COLOR

One could justifiably suspect that general collectors might make more effort to collect and preserve an unusually black or unusually buffy fox squirrel and

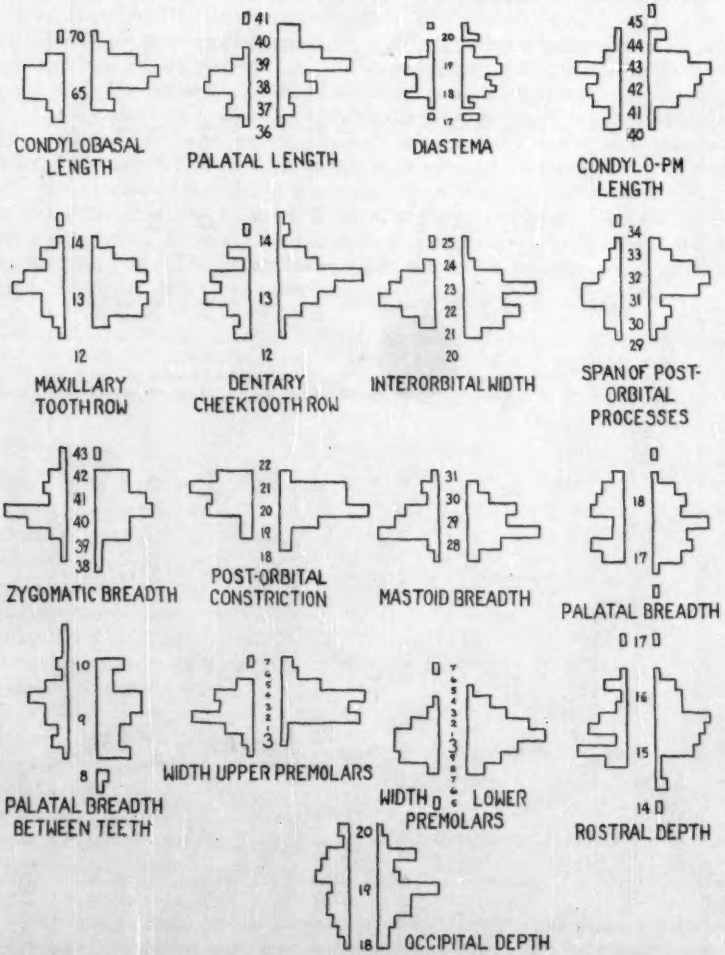


Fig. 3.—A twin histogram compares the measurements from 36 male (left) with those from 55 female (right) fox squirrels for each of 17 skull characters. These are of the central Florida subspecies, from various parts of its range. Material used here has a tooth-wear classification of five or higher. All numbers in these histograms represent millimeters, or millimeters and tenths of millimeters.

TABLE 2.—Color comparison of 78 male and 95 female fox squirrels from central Florida.

	White or whitish		Tan		Buff		Agouti		Blackish agouti		Black	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
front feet	1	2	54	40	6	18	12	7	6	15	21	22
front digits	21	8	62	61	5	8	8	17	1	3	6	7
front wrists	3	0	37	41	10	11	36	20	4	11	21	22
front legs	1	0	20	26	9	6	64	61	13	16	21	21
hind feet	1	0	27	19	14	13	45	42	15	13	30	39
hind digits	13	7	56	51	8	14	16	14	9	11	3	5
tail hair, tips	23	23	65	60	8	15	0	0	0	0	5	2
tail hair, basal bands	4	2	17	20	78	72	0	0	0	0	1	5
lips	96	92	3	5	0	0	1	0	0	0	0	0
chin	38	39	30	32	3	4	13	8	3	2	13	16
ear tips, inside	76	64	21	32	0	2	4	3	0	0	0	0
ear tips, outside	65	56	26	34	0	2	9	10	0	0	0	0
rostrum	100	93	0	6	0	0	0	0	0	0	0	2
cheeks	0	0	0	2	0	2	18	21	35	32	47	50
crown	0	0	0	0	0	0	0	0	0	3**	100*	97
nape	0	0	0	0	0	0	59	55	15	20	26	25
back	0	0	0	0	0	0	83	68	8	13	13	19
sides	0	0	0	0	0	0	94	92	3	2	8	6
venter	5	5	35	44	40	31	1	2	0	2	18	17

* two with stars, two black & agouti
** one starred

thus bias a sample on color. Since F. L. Small collected the 34 specimens from Citronelle, Citrus County, all in about six months, however, in the present writer's opinion Small was collecting every one that he could get regardless of color phase. The writer collected 29 specimens at Welaka, Putnam County, without regard to phase. These two small series were compared to the whole central Florida series of 176 specimens as to incidence of the various colors on 19 pelage areas in table 4. In this comparison it appears that each of the smaller samples is often at variance with the large one. The disagreement of the smaller samples is usually greater with each other, however. Apparently the entire central Florida sample is not badly biased.

Table 4 also reveals which pelage areas as the most stable in color. Whitish nose and ear tips have been regarded by most authors as the most constant color characters of *Sciurus n. niger*, but in this central Florida material we find the stablest characters to be in this order: black crown, white or whitish nose, agouti sides, agouti back, and buff basal bands of tail hairs. The variety of color dominating these most stable areas is interesting in itself: black, white, agouti, and buff. The pelage areas which vary most in color are front feet, hind feet, wrists, chin, cheeks, and venter.

TABLE 3.—Individual variation in skull characters of central Florida fox squirrels having a toothwear class of five or higher. Mean, standard deviation, and coefficient of variation are shown in millimeters.

Character	Sample	Mean	Stand. dev.	Coeff. var.
width lower premolar	92	3.09	0.0575	0.0186
width upper premolar	93	3.31	0.0498	0.0150
maxillary toothrow	91	13.20	0.4030	0.0305
dentary cheek-tooth row	91	13.31	0.4167	0.0313
rostral depth	92	16.60	0.5230	0.0315
palatal breadth incl. teeth	80	17.67	0.4733	0.0216
diastema	92	18.66	0.7830	0.0379
occipital depth	83	19.03	0.6421	0.0337
postorbital constriction	91	20.56	0.7074	0.0344
interorbital width	88	22.86	0.8557	0.0374
mastoid breadth	79	29.17	0.7873	0.0270
span post-orb processes	77	31.84	1.0079	0.0313
palatal length	76	38.70	0.9935	0.0205
zygomatic breadth	84	40.81	1.0011	0.0245
condylopremolar length	82	42.74	0.7747	0.0181
condylobasal length	70	66.85	1.5760	0.0236

What percentage of the population each different color phase represents, pertains to geographic more than individual variation; hence these are presented under the heading of geographic variation and summarized in table 5.

Melanism.—All studied areas of the pelage in this series, excepting nose and ear tips, are sometimes black. Inspection of table 4 reveals that of the 15 pelage areas which are subject to being black, the order from most often black

to least often black is crown, cheeks, hind feet, nape, front feet, front legs, venter, back, chin, sides, front digits, hind digits, tips of tail hairs, basal band of tail hairs, and rostrum. None of the 176 central Florida specimens had

TABLE 4.—Individual variation in color among central Florida fox squirrels.

	White and whitish			Tan			Buff		
	Wel.	Cit.	All	Wel.	Cit.	All	Wel.	Cit.	All
front feet	....	....	1	48	59	49	24	6	13
front digits	3	9	14	59	59	61	17	6	7
wrists	....	....	1	48	38	39	17	6	11
front legs	....	....	1	38	21	22	10	6	9
hind feet	....	....	1	28	35	23	28	6	14
hind digits	....	6	10	48	56	56	24	3	11
tail hairs, tips	10	29	23	55	59	62	34	6	12
tail hairs, bases	....	6	2	8*	32	18	92*	59	76
lips	100	94	97	....	6	4	....	....	....
chin	45	21	39	21	53	34	17	....	3
eartips, inside	41	53	68	59	47	28	....	....	2
eartips, outside	52	53	64	62	44	26	....	....	....
rostrum	93	97	95	7	3	4	....	....	....
cheeks	....	....	1	....	3	....	7	....	2
crown	....	....	....	....	....	....	....	....	....
nape	....	....	....	....	....	....	....	....	....
back	....	....	....	....	....	....	....	....	....
sides	....	....	....	....	....	....	....	....	....
venter	7	3	5	24	62	43	59	15	32

	Agouti			agouti Blackish			Black		
	Wel.	Cit.	All	Wel.	Cit.	All	Wel.	Cit.	All
front feet	3	3	9	3	9	11	21	26	21
front digits	7	24	14	7	3	2	14	....	6
wrists	17	24	27	7	6	7	14	26	22
front legs	72	59	65	17	12	14	10	24	20
hind feet	62	38	43	3	....	13	21	41	34
hind digits	10	24	16	14	15	9	7	....	5
tail hairs, tips	....	....	....	....	....	....	....	6	4
tail hairs, bases	....	....	1	....	....	....	....	3	2
lips	....	....	....	....	....	....	....	....	....
chin	7	3	11	....	6	2	14	18	14
eartips, inside	17	....	2	....	....	....	....	....	....
eartips, outside	28	3	7	....	....	....	....	....	....
rostrum	....	....	....	....	....	....	....	....	1
cheeks	21	41	20	48	24	33	38	35	49
crown	....	3	....	....	3	3	100	97	98**
nape	66	71	58	21	9	17	24	21	25
back	97	85	80	7	9	11	21	15	18
sides	100	91	94	....	....	2	....	12	7
venter	3	....	1	....	....	1	7	21	17

Wel.=% of Welaka series (29)
Cit.=% of Citronelle series (34)
All=% of whole central Florida series (176)
** 2 of these are starred and 2 blazed
* sample is only 26 here

black ear tips. There was only one, a 400 mm nestling from Marion County (M 383) whose rostrum was recorded as blackish.

Black-bellied phase.—Careful tabulation and checking has demonstrated clearly that no two fox squirrels of the 46 blackest central Florida specimens are entirely alike in the distribution of black, partly black, and blackish agouti to all pelage parts. However, comparison with regard only to pelage areas which are entirely black does show some conformity. It is rather interesting, too, that these data confirm the existence of a distinct and common phase which is the phase no. 3 described by Audubon and Bachman (1851) and which has been ignored by more recent authors. This may be called the black-bellied phase. It is represented in the central Florida material by eleven individuals which conform perfectly to the following pattern: entirely black on belly, cheeks, crown, wrists, and front legs; not entirely black (*i.e.*, may be some other color and/or partly black or blackish agouti) on sides, back, digits, and bases of tail hairs; white or whitish on rostrum and ear tips; nape and feet may be black or not. Examples are MCZ1968, USFWS79136, USNM-111351 and 111376, M168, CMNH14945, and ANSP8670. There are seven more individuals which disagree with this pattern only in some small pelage area. If these be included with the properly black-bellied phase individuals, the resulting group includes 18 individuals.

Black phase.—The black phase as described by Audubon and Bachman (1851), Howell (1919), and Hamilton (1943) has been considered uncommon by other authors and is very scarce in this central Florida material. Only one of this lot agrees entirely with Bachman's or Howell's description, and none quite does with Hamilton's. However, if the description be modified to permit something other than black on the digits and feet two specimens do fit (MCZ1967 and USFWS 79142). So constituted, this description is: all pelage parts black excepting nose, ear tips, feet, and digits which are each white, partly white, or agouti. Seven are so near to being black phase that it is not certain what other phase may be represented. Of specimens intermediate between black phase and other identifiable phases, black dominates tan six times, gray-white five times, and buff five times. In 11 other intermediates black is considered to be dominated by the other phases. The 23 black-dominated intermediates, 18 black-bellied phase, and two black phase total 43 especially black individuals. From this we infer that on the average we may expect strong melanism in one out of four fox squirrels encountered in central Florida.

But whether they be strongly melanistic or not, table 4 shows that virtually all central Florida specimens have black crowns, half have black cheeks, one-third have black hind feet, and front legs, wrists, and front feet are each black a fifth of the time. The incidence of traces of melanism is such that 53% of the sample has some solid black on at least one pelage part other than the crown.

Buff phase.—There are five specimens which agree in being buff on the venter, basal band of tail hairs, front and hind feet, front and hind digits, and wrists, and in having agouti sides and back, black crown, and white or whitish rostrum. These are M89, M213, M235, MCZ1962, and ANSP17196. This, however, amounts to too small a proportion of the buffier specimens. It seems

much more useful to recognize as buff phase any individual which possesses a buff venter and buff basal band of tail hairs. This combination occurs in 48 individuals of the central Florida sample. Some examples: MCZ1953, 1961, 1964 and 1984; CMNH14944 and 65575; and USNM111269, 111278, 111340, 111380, 193937, and 193938. An exceptionally intense buff specimen is M393.

Table 4 shows that the basal band of tail hairs is buff in three-quarters of the sample, and that the venter is buff in one-third. The next most often buff pelage area is hind feet which is only 14%. Although table 4 does not show it (for reasons stated already under Color Description), buff affects all the pelage areas which black does except the crown. It is interesting that while buff occurs only about half so often as does black on the legs and feet, its occurrence on the digits exceeds that of black, and incidence on the venter and basal band of tail hairs exceeds that of black by far.

All five of the skins which are intermediate between buff phase and black phase are dominated by the black, but in the six intermediates between buff phase and tan phase four are dominated by buff and two by tan.

Tan phase.—The most abundant and therefore the "common" color phase in this central Florida material is a tan phase which possesses 1) a venter of tan, 2) basal band of tail hairs of buff or tan, 3) back and sides entirely of agouti, and 4) digits, feet, wrists, and legs neither darker than agouti nor more intensely colored than tan. Fifty-five specimens agree entirely in this. Examples are M167, MZUM58134, USFWS79133, USNM193933, MCZ1360, CMNH4735, AMNH22688, and CM16526.

On those skins which are intermediate between tan phase and other color phases, tan dominates black twelve times, gray-white four times, and buff phase twice. Table 4 shows that in the central Florida material tan is the most frequent color for venter, tips of tail hairs, front and hind digits, front feet, and wrists. This clearly makes it second only to agouti as the most frequent color for the greatest area of the pelt.

There are some exceptional features of casual interest in the non-diagnostic pelage areas of some perfect tan phase skins. The crown fails to be entirely black in four cases. It is starred or blazed with white in two instances, blackish agouti in one, and in the last constricted to a small circular black patch. The rostrum is tan twice instead of white or whitish. The ear tips, inside and out, are tan instead of white or whitish in eight specimens.

Gray-white phase.—The gray-white color phase in the fox squirrels of central Florida is exceedingly rare. This phase is constituted by 1) white or whitish venter; tan, white, or whitish basal band of tail hairs; 2) agouti or pale agouti sides, back, and nape; 3) blackish agouti cheeks; 4) no part of limbs darker than agouti, or more intensely colored than tan; 5) crown black; 6) rostrum and ear tips white. Only one central Florida specimen quite fits this phase description, from Gilchrist County collected by Byrum Cooper 5 miles north of Bell (M391). Differing only slightly from it, however, are one from Gilchrist County 11 miles northeast of Trenton (M397), Tarpon Springs, Pinellas County (ANSP7973), and Lake Geneva, Clay County (ANSP1922).

This phase is the one which Audubon and Bachman (1851) describe as the "grey variety." They describe the feet and basal band of tail hairs as

white, but the *Sciurus n. niger* material that I have examined from the Santee River area of South Carolina shows in some cases a faint wash of pale tan on these parts. Howell (1919), who calls this phase the "gray phase," is certainly referring to this phase in typical *niger* where he states, "Some specimens in this phase have the feet and under side of the tail buff, thus approaching the next darker phase." I feel confident from his other usages of the word buff that in this case he meant what is here called tan. And since Audubon and Bachman (1851) contend that intermediates are rare in *Sciurus n. niger,* it seems best to include tan feet and tan basal bands of tail hairs in gray-white phase.

Albinism.—In 1946, L. S. Barstow, then superintendent of schools in Putnam County, told me of two entirely white fox squirrels which he caught several months apart in 1931 between East Palatka and Hastings in Putnam County. He captured the second within two miles of where he had taken the first. The following year he caught another entirely white fox squirrel in the same locality. This one was evidently younger than the first two. He considered the first two to be litter mates. Two of these squirrels lived in captivity about four years, and were seen by many people. Two photographs which Mr. Barstow lent me show the squirrels to be entirely white, and one eye is in good enough focus to show that the iris is as light as the animal's pelt. Mr. Barstow told me of another white fox squirrel which Zernie Solano of Elkton, St. Johns County, had caught about 1930 in the same general vicinity and kept captive. The writer met Solano once and verified this but could obtain no further detail.

In June, 1946, Emory Ferrell, then a game warden in Putnam County, told me of a pure white fox squirrel with pink eyes which Willy Rogero of San Mateo had killed near there in 1945 or 1944.

Florida Wildlife for January 1951 (p. 26) published an account of an albino squirrel killed in the Ocala National Forest by Floyd Arnold of Ocala. In a letter of January 26, 1951, Arnold informed me that the animal's eyes were pink and that it measured "from tip of nose to end of tail," twenty-two inches. It was killed at Buckskin Pond near a hammock on December 10, 1950. I find a "Buckskin Prairie" mainly consisting of two ponds in the northern part of the forest immediately east of Lake Delancy (or lat. 29° 25′ and long. 81° 45′). Adult fox squirrels in this part of Florida average about 24¾ inches in total length, but adult gray squirrels (*Sciurus carolinensis*) probably average no greater than 16 inches in length (Moore, 1946). Even if Arnold measured to the end of the tail hairs, 22 inches makes it more likely a fox squirrel than a gray.

W. S. Swilley of Paolita Station, Monroe County, tells me that he and his brother trapped a white fox squirrel in the early 1920's between Jasper and Lake City, and I have talked to a well-informed man from Tampa who told me of seeing a pure white wild fox squirrel at very close range in a forested part of Hillsboro County.

GEOGRAPHIC VARIATION

Fox squirrels in Florida, in spite of their extreme color variation, separate

rather easily into three geographic groups on the basis of color and size. These are west, central, and south Florida populations.

WEST FLORIDA

Although the color sample of the west Florida population amounts to only 18 skins, these agree quite well with typical *Sciurus n. niger* from southeastern South Carolina. Only one is black phase (M422) and one tan phase (AS516), whereas five are intermediate between the black phase and gray-white, and eleven conform perfectly to the above description of gray-white phase. Examples of gray-white phase are M438, M425, USNM257963, and MZLS2401. According to Audubon and Bachman (1851), who were best acquainted with *Sciurus n. niger* in its type locality, the gray-white phase is the most common phase in that race. The series of five specimens which the writer has examined from the vicinity of the Santee Post Office and the Santee River, South Carolina, contains one black-bellied phase (RMAG2636) and four gray-white skins (MCZ20234, 20235, and 20236, and RMAG 2635). The proportion of the population sample represented by each color phase is shown in table 5.

TABLE 5.—Percentage of various color phases and, in parentheses, total percentage of individuals dominated by the color of the indicated phase, in races of fox squirrels in Florida.

	black	black-bellied	buff	tan	gray-white	sample
niger	5(33)	0	0	5(5)	61(61)	18
shermani	1(24*)	6	27(27)	31(41)	1(2)	176
avicennia	11(27)	0	35(68)	4(4)	0	54

* Includes 6% black-bellied phase, 4% near black-bellied phase, 1% black phase, and 13% near black phase.

The distribution of *Sciurus n. niger* to west Florida should be no surprise, since Howell (1921) reports six specimens of this race from Abbeville in southeastern Alabama, and Lowery and Davis (1942, p. 156) report three specimens from Thomasville, Georgia. Both of these localities are only a short distance north of the border of west Florida. From Newton, Georgia, a locality about midway between the above places, the writer has examined a series of eight skins collected by E. V. Komarek. Perfect conformity to the common gray-white phase of *Sciurus n. niger* is shown by all eight.

The vicinity of the Suwanee River is considered to be the eastern edge of the area of intergradation between this form and the next. See fig. 4.

CENTRAL FLORIDA

Sciurus niger shermani, new subspecies

Type.—Female, adult, skin and skull, no. 483; University of Florida, Department of Biology; 2 miles E. of University of Florida Conservation Reserve, Welaka, Putnam County, Florida; September 29, 1946, collected by Joseph C. Moore, original number M167.

Range.—Most of peninsular Florida, extending northward to the state

line at least in Nassau County, and probably on into southeastern Georgia, westward into Gilchrist (M398) and Levy counties (PGP134), southward probably to the vicinity of the Caloosahatchee River (at least to Highland, USFWS64022, 64023, and 64024, and Hillsborough counties) on the west, and south to Jupiter, Palm Beach County, on the east coast (CMNH14943, 14944, and 14945). See fig. 4.

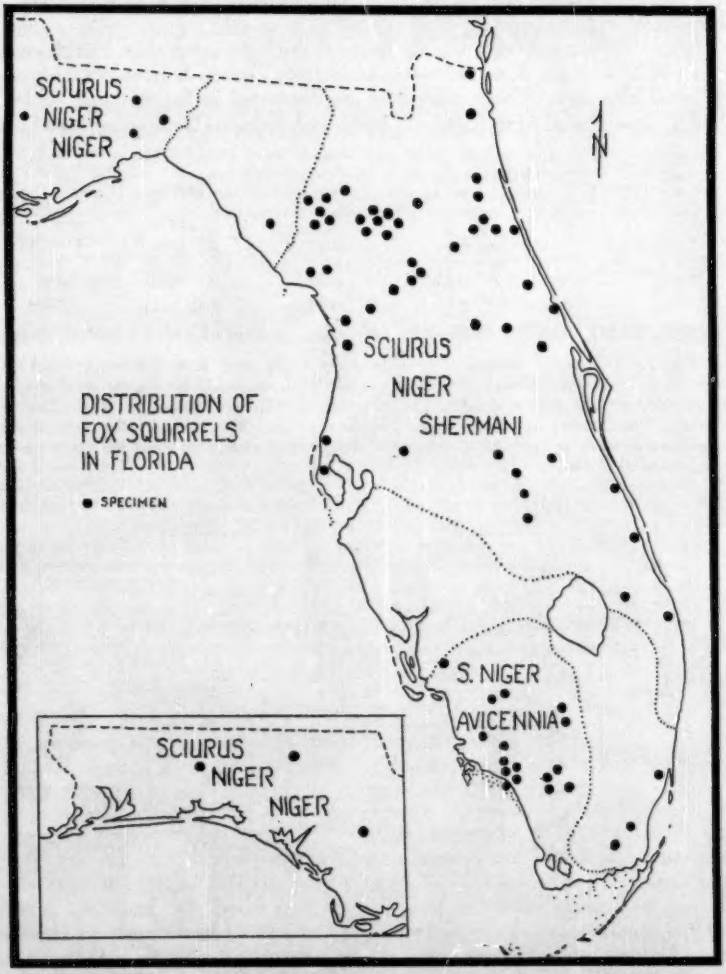


Fig. 4.—Geographic distribution of fox squirrels in Florida. Dotted lines hypothetically separate ranges of subspecies from areas of intergradation. Each black spot represents a locality from which fox squirrel material has been examined by the author.

Diagnosis.—Color. The race differs from typical *niger* in that its common phase is tan rather than gray-white phase. The color of the common phase also distinguishes *shermani* from the race with which it intergrades on the south, *avicennia*, in which the common phase is buff (table 5). White on the ears is more often restricted to the tips and more frequently replaced by tan in *shermani* than in *niger* or *avicennia*. The feet, excluding digits, are commonly tan and occasionally buff in *shermani* but very rarely white as is common in both *niger* and *avicennia*.

Size.—While only very slightly larger in skull characters than Florida specimens of *S. n. niger*, *S. n. shermani* considerably exceeds *S. n. avicennia* in size of skull characters. These differences are illustrated in figures 5, 6. Tables 6 and 7 show a marked difference in body measurements between *shermani* and

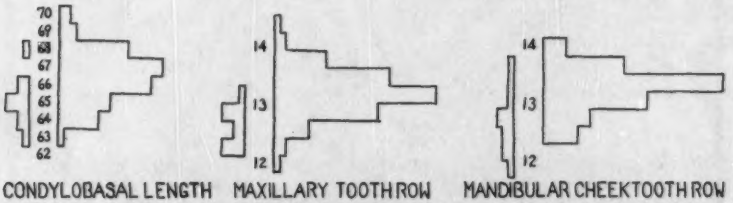


Fig. 5.—Differences between *Sciurus n. niger* (left) and *S. n. Shermani* (right) in three skull characters. These differences evident here, obviously insufficient in themselves to differentiate the two subspecies, are presented to illustrate the extent of variation involved. The samples are from 11 west Florida *niger* and 87 *shermani*, all with toothwear classification of 5 or higher. Condylobasal length is indicated in mm, the other two in mm and tenths of mm.

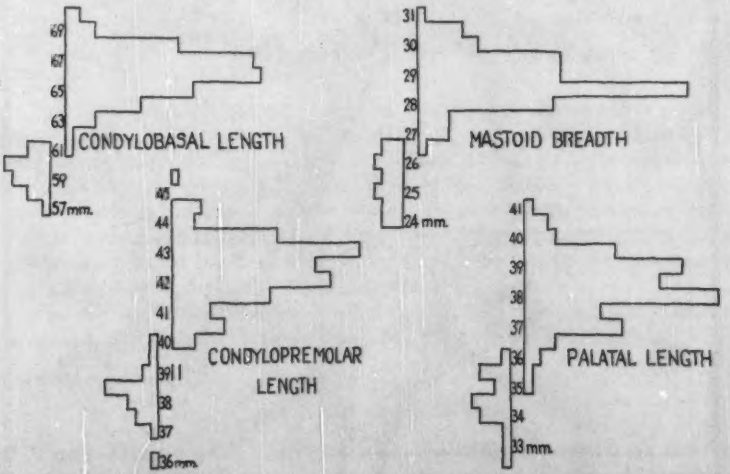


Fig. 6.—Twin histograms illustrate the difference between a sample of 26 adult *Sciurus niger avicennia* (left) from a sample of 140 adult *S. n. shermani* (right) in four skull characters. The only criterion of adultness used here was possession of fully erupted permanent premolars.

avicennia but on very little data. Individual variation in size of skull characters of *shermani* is shown in table 3.

The above reported investigation of individual variation dealt with 176 study skins and 93 fully adult skulls from "central Florida," which was all of the material available to me from within the range of the population now designated *Sciurus niger shermani*, and hence applies entirely and strictly to this new race. The name *shermani* recognizes H. B. Sherman whose research and guidance of graduate students have greatly increased knowledge of Florida mammals.

TABLE 6.—Measurements in millimeters and weight in grams taken by the writer from freshly-killed typical *Sciurus niger shermani* whose tooth-wear class is at least five. Head and body length was obtained by subtracting tail length from total length. Measurements of tails which had apparently suffered accidental abbreviation are not used here excepting in the case of the type.

measurement	type	topotypes	sample
head and body	326	315 (300-335)	20
tail	284	310 (302-328)	16
hind foot	84	85 (80-90)	19
ear	18	17.5(15-19)	19
weight	1077.8	1072.6(925-1180.5)	18

TABLE 7.—Measurements made in millimeters of specimens of *Sciurus niger avicennia* by W. S. Brooks (5), T. Donald Carter (4), A. H. Hardisty (1), A. H. Howell (2), Roy V. Komarek (5), and A. Schwartz (2). The length of head and body was obtained by subtracting length of tail from total length. All data from specimens with fully erupted permanent premolars, but only the last line is of toothwear class of five or higher. A topotype, MCZ18046, was excluded from the tabulation because of its exceptionally small size (493-227-71-28), even though it was recorded to have fully erupted permanent premolars. The topotypes used are MCZ18043, 18044, 18045, 18048, and 18049. Only the class 5+ data are directly comparable to those for shermani in table 6.

	head and body	tail	hind foot	sample
type	275	260	75	1
topotypes & type	266(255-286)	246(237-260)	73(72-74)	6
all *avicennia*	281(255-308)	259(237-276)	75(71-80)	17
class 5+	278(262-301)	261(241-276)	76(73-79)	4

Means of distinguishing mammalian subspecies are often such that not every specimen can be given its proper subspecies name. Where distinguishing criteria are based only upon size, specimens of immature individuals cannot properly be determined to subspecies. Likewise, where distinguishing criteria are based only upon color, material which is strongly albinistic, erythristic or melanistic usually cannot be properly identified to subspecies. The abundance of aberrantly colored individuals in *Sciurus niger shermani* has long obscured the important fact that in its ordinary and predominant color phase it is distin-

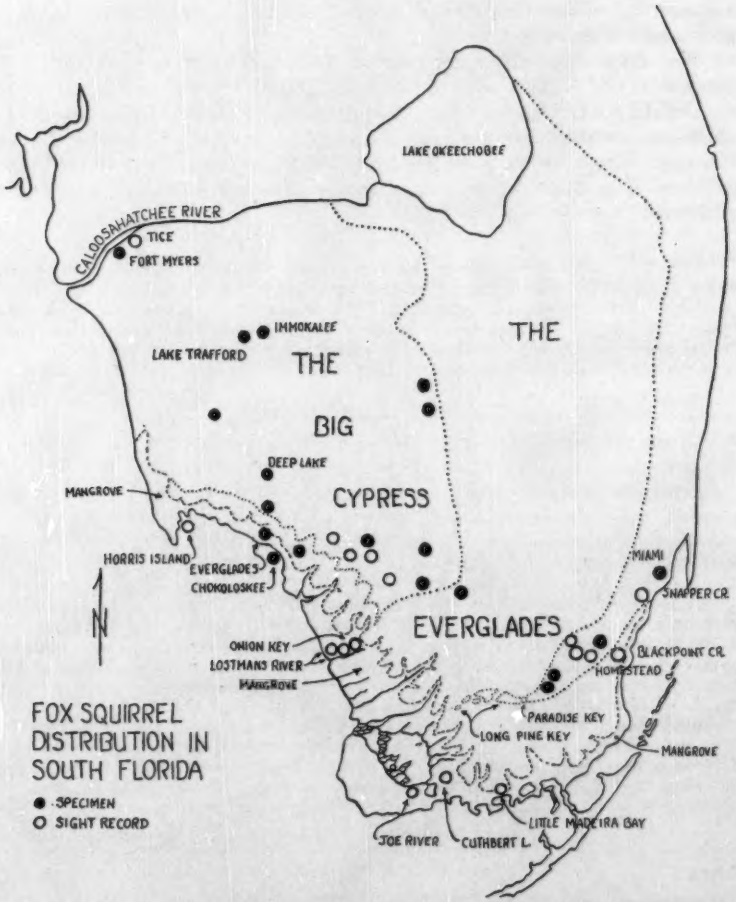


Fig. 7.—Distribution of the fox squirrel in relation to the Everglades, the Big Cypress, the mangrove, and the finger of pinelands pointing southwestward from Miami. Specimens from south of the Caloosahatchee River and west of the Everglades are *Sciurus niger avicennia*. So are ones from the mangrove, but those from the pinelands between Miami and Long Pine Key are intergrades between *avicennia* and *shermani*.

guishable from *S. n. niger*. *Sciurus n. niger* and *S. n. shermani* are distinguished on the basis of color, and erythristic and most melanistic examples of them may not be identified to subspecies. The following key, however, will distinguish 91% of the remaining skins in an average sample of *shermani*. Since *avicennia* is distinguished from *shermani* on the basis of skull characters, adult individuals may be assigned to one or the other subspecies irrespective of color phase.

KEY TO SUBSPECIES OF FOX SQUIRRELS IN FLORIDA

A. Venter white or whitish ..... *S. n. niger*
AA. Venter tan, buff, or black ..... B
B. Condylobasal length less than 62 mm, and mastoid breadth less than 27 mm ..... *S. n. avicennia*
BB. Either or both characters larger C
C. Venter tan ..... *S. n. shermani*
CC. Venter black or buff ..... indistinguishable

SOUTH FLORIDA

Howell (1919) conceived *Sciurus niger avicennia* to be restricted to ". . . the southwest coast of Florida . . . in the damp, dark forests of black- and red-mangrove which extend practically without a break from Marco Pass to Cape Sable and around the southern end of the peninsula to the shores of Biscayne Bay on the east coast." At that time there were specimens of fox squirrels available in museums from Fort Myers, Lake Trafford, Immokalee, Deep Lake, Chokoloskee, head of Barnes River (now Lopez River), Miami, and west of Florida City. See fig. 7. These specimens, numbering 16, and the type were probably all studied by Howell and except for the type doubtless constituted the "numerous specimens examined from the pine and cypress forests of Lee and Dade County. . ." which Howell considered to be ". . . variously intermediate between *niger* and *avicennia*, many of them indistinguishable from *niger*, although always smaller." While concurring in the material from the pinelands near Florida City and Miami being intergrades (now necessarily with *shermani*), the present writer includes those from all of the other above mentioned localities as definitely *avicennia* (figs. 4, 7).

As already mentioned, this subspecies is known in the literature from only one specimen, the type. Fifty-six skins from south of the Caloosahatchee River and west of the Everglades proper have been available to me in the present study and are considered to be *Sciurus niger avicennia*.

Color.—Six of the 54 specimens are excellent examples of black phase. They are all characterized by the pelage being entirely black excepting for the lips, rostrum and ear tips, which are white or whitish; the front and/or hind feet which may be blackish agouti; and the front and hind digits which may be white, whitish, or blackish with white hairs. (Examples are JAW427, MCZ18043 and 18045.) This represents about 10% of the *S. n. avicennia* sample, as shown in table 5.

Nine specimens of *avicennia* are almost black enough to be black phase. Nine others, still, appear to be intermediate between black phase and buff phase but are dominated by the black. Thus, the black and black-dominated specimens of *avicennia* total 24 or 47% of the sample.

Nineteen skins are good buff phase. This phase in *avicennia* is characterized by buff venter and basal bands of tail hairs; *white* digits, lips, nose, and eartips; black or blackish agouti crown, agouti or blackish agouti back. Examples are USFWS231602, MCZ18049, USNM255552, and AMNH145132. Four specimens differ from this pattern only slightly. Three other specimens appear to be intermediate between buff phase and black phase but are dominantly buff. Therefore, the truly buff phase constitutes about 35% of the *avicennia* sample, but 37 individuals or about 68% are dominated by buff.

Two of the 54 *avicennia* specimens are tan phase. These agree in having tan venter and buff basal band of tail hairs; white lips, rostrum, and ear tips; agouti cheeks, nape, back, and sides; limbs white to tan. These are MCZ18050 and JAW430.

Size.—The race *Sciurus niger avicennia* measures smaller on the average than *S. n. shermani* in all seventeen skull characters described. Since skulls classifying high on the toothwear scale are few in the *avicennia* material, presence of fully erupted permanent premolars is the only criterion used in selection of adult material for this comparison. Figure 6 illustrates by means of twin histograms the difference between skull size in *avicennia* and *shermani* in the four characters in which the difference is greatest.

The writer measured only two specimens of *avicennia* in the flesh, both adult males. One taken in the Big Cypress in Collier County a few miles from the borders of Hendry and Broward counties, on February 1, 1952, measured: head and body length 295, tail 257, and hind foot 75 mm. One (M454) taken October 16, 1951, on the Tamiami Trail half way across the Everglades proper, measured: head and body length 265, tail 266, hind foot 77 mm, and weighed 1049 grams. This one was probably traveling east through the row of Australian pines (*Casuarina*) which are planted for a windbreak beside this highway, or may have been an escapee from an Indian Camp, which had such captives, a couple of miles west. Table 7 provides some further data on body measurements of this form.

Origin.—The type and a series of eight topotypes of *avicennia* include 4 black phase, 1 buff phase, 1 tan phase, 2 buff-dominated intermediates between buff and black phase, and 1 black-dominated intermediate between black phase and tan. There is an inordinately large proportion of black phase in this little sample from the mangrove. Also, this type material averages slightly smaller in several skull characters than material from the nearby Big Cypress. It is even true that the mangrove forest is rather consistently separated from the pine and cypress by a belt of salt marsh a mile or more wide which certainly serves to some extent as a barrier isolating the population in the mangrove. The dark, saline swamp community of mangrove forest may be selective for the black phase and for small size.

A better explanation of the origin of the subspecies *avicennia* may be that a population of fox squirrels of the mainland became isolated by a rise of the ocean to a stage known as the Pamlico sea (Cooke, 1945). On a large, oval island separated from the mainland to the north by a five-mile strait where the Caloosahatchee River is now, this population would have lived under conditions believed to be very little different from those prevailing today (Simpson, 1929). During this isolation some 25,000 years ago these fox squirrels would have become differentiated during Pamlico time. Like many other mammals restricted to islands (Hesse, Allee, and Schmidt, 1937), they became reduced in size. When the sea dropped to present levels, this population would presumably have spread, in the wake of suitable ecological conditions, to their present range and interbred with the mainland form upon reaching it along the Caloosahatchee River. At the other end of its range it would have spread into the mangrove where the apparent partial isolation would have accelerated the natural selection for black phase by the dark forest environment.

Distribution factors.—Figure 7 shows the distribution of *avicennia* in detail. The Everglades north of the Tamiami Trail provides an impassable barrier to east-west movement of fox squirrels. From about there south, however, tree-islands are more abundant and it appears possible that during an exceptionally high population level a few, wandering across glades from tree island to tree island, might cross the Everglades. Men with much experience in this portion of the Everglades, though, advise me that observation of a fox squirrel out in these Everglades tree islands away from the cypress is rare. Farther south, as illustrated in figure 7, the eastern pinelands reach out through the glades toward the mangrove. According to Bailey (1930) the fox squirrel occurred here east and west of Paradise Key. Nearly all of the salable pine timber has been removed since that time, and if the fox squirrel survives today in the pinelands anywhere south of Miami, it is exceedingly rare. However, the western tip of these eastern pinelands comes within a mile or two of the mangrove and the gap is studded with tree islands. This seems the most likely avenue of intergradation between *avicennia* and *shermani* of the east coast.

As quoted above, Howell has implied that *avicennia* may occur in the mangrove all the way around the south end of the mainland. Figure 6 shows localities where fox squirrels have been observed, indicating that this is possibly true. Some discussion seems desirable here. The mangrove area includes many square miles of forest of mixed red, black, and white mangrove trees (*Rizophora mangle, Avicennia nitida,* and *Laguncularia racemosa*) in that order of abundance. I do not believe that this saline littoral swamp forest provides food and water for the fox squirrel, certainly not the year around. On occasional slight elevations within the mangrove swamp, such as the few Indian mounds and beach dunes, hammock growth of broadleaved, evergreen hardwood trees occur which provides a variety of fruits and seeds on which the squirrels might feed, and leaves from which they might lick the dew without getting salt. In large areas the mangrove is dwarfed, and there is virtually nothing but the bush-size red mangrove growing on mud, extending for miles and unbroken excepting by a patternless labyrinth of waterways. At the headwaters of the mangrove rivers and near where the mangrove area and sawgrass glades area meet, there are often tree islands within the shrubby mangrove. Some of these are hammocks occupying slight elevations, others are bayheads of freshwater swamp trees believed to occupy depressions filled in with peat. These also appear to provide a variety of fruits and seeds which might help sustain a thin population of fox squirrels. The tenuousness of the coastal strip of mangrove from Little Madeira Bay eastward and northward along Biscayne Bay, and the large proportion of the mangrove which is dwarfed there, appear to offer only a most dubious fox squirrel habitat or travel route. Any mangrove fox squirrels along Biscayne Bay, therefore, are presumed to have been transported by man across the Tamiami Trail, or to have developed there secondarily from the hybrid population in the adjacent Miami rockland pine forests.

Occurrence.—The fox squirrel is extremely rare in the mangrove area south of the Lostmans River. A severe hurricane passed directly through this area in 1935 and destroyed many square miles of mature mangrove forest, much

of which after 19 years still stands as a forest of dead snags with no evidence of recovery or reproduction. This hurricane doubtless destroyed most of the fox squirrels in the Cape Sable region and rendered large areas no longer suitable for their occupation. Their scarcity is such that it seemed worth while to report (Moore 1954) details of the few observations which I recorded during three years of field work in the area, even though all were second hand. The localities for these are indicated on figure 6.

Erwin C. Winte, a ranger in the Everglades National Park and former local game warden, observed a fox squirrel in March of 1932 in the oak ridge on Horris Island, one of the northwesternmost of the Ten Thousand Islands.

The rarity of fox squirrel occurrence in the Miami rockland pine area and improbability of its survival of man's development there, warrant details also. Erwin C. Winte told me of two black fox squirrels whose tanned skins he saw after they had been killed on Black Point Creek in the 1948 hunting season, probably in December. H. E. Hemans of East Newton Road, Homestead, told me of seeing a fox squirrel on an avocado tree back of his residence on September 21, 1949. Darwood B. Sutton lent me the skin of a fox squirrel which a visitor had knocked from a tree beside Sutton's house about a mile northwest of Princeton on May 13, 1951. Roy O. Woodbury of the Botany Department, University of Miami, killed a large, gray squirrel in the pinelands about 5 miles west of Princeton back in about 1924. He is concerned that this one may have been too *large* to be a fox squirrel. Mr. Woodbury also saw a black phase fox squirrel in the hammock by Snapper Creek Canal a mile from where it enters Biscayne Bay south of Miami, in the summer of 1948 and again once more recently.

It is notable that in most of the recorded fox squirrel observations in the mangrove, the animals were described as black. Willard E. Dilley, park naturalist of the Everglades National Park, observed a black fox squirrel in the town of Everglades between December 1 and 7, 1947. These observations together with the proportion of black-dominated specimens in the mangrove area material, and the partial isolation of the mangrove from the Big Cypress area, suggest the possibility that subspecific differentiation between the fox squirrel populations of these two areas may be taking place.

SUMMARY

Three subspecies of fox squirrels in Florida are recognized: *Sciurus niger niger* west of the Aucilla River; *Sciurus niger shermani* described as new east of the Suwannee River and north and east of a line passing from Tampa Bay through Lake Okeechobee; and *Sciurus niger avicennia* occupying the mangrove, the pinelands, and the Big Cypress west of the Everglades and south of the Caloosahatchee River. The new form is distinguishable from *S. n. niger* in 91% of the *shermani* material other than erythristic and strongly melanistic individuals.

Five color phases are recognized in Florida fox squirrels: black, black-bellied, buff, tan, and gray-white. Gray-white is the common color phase of *Sciurus n. niger* but occurs rarely in *shermani* and apparently not at all in *avicennia*. Tan is the common color phase of *shermani* but occurs rarely in *avicennia*. Buff is the common color phase of *avicennia* but occurs frequently in *shermani*. Black phase occurs in all three subspecies, but with the greatest

frequency in *avicennia*. Black-bellied phase occurs frequently in *shermani*. The incidence of strong melanism in *shermani* is 24%, and that of strong erythrism 27%. Albinism occurs in *shermani*.

Sciurus niger shermani appears to be the largest of the three Florida forms. *S. n. avicennia* is the smallest of the three Florida forms.

Comparison of male and female fox squirrels of *shermani* in measurement of 15 skull characters and color of 19 areas of the pelage revealed no sexual dimorphism which would distinguish any considerable part of the population as to sex.

Presence of fully erupted permanent premolars proved of some value in selecting adult material, but selection on a basis of a tooth-wear class of five or higher is considered of greater worth.

Examination of individual variation in 16 skull characters of *Sciurus niger shermani* revealed greater stability in several rarely measured skull characters (width of upper and lower premolars, condylopremolar length, and palatal breadth including teeth) than in most of those traditionally used. In distinguishing *avicennia* from *shermani*, however, only condylopremolar length proved equal in value to the traditional condylobasal length, palatal length and mastoid breadth.

REFERENCES

ALLEN, DURWARD L. 1942—Populations and habits of the fox squirrel in Allegan County, Michigan. Amer. Midl. Nat. 27(2):338-379.

AUDUBON, J. J., AND JOHN BACHMAN 1851—The viviparous quadrupeds of North America. Vol. II.

BAILEY, HAROLD H. 1930—Correcting inaccurate ranges of certain Florida mammals and others of Virginia and the Carolinas. Bull. No. 5, Bailey Mus. and Lib. Nat. Hist., Miami, Florida.

CHRISTY, BAYARD H. 1928—Bird notes from southern Florida. Auk. 45:283-289.

COOKE, C. WYTHE 1945—Geology of Florida. Florida Geol. Surv. Bull. 29:1-339.

HAMILTON, WILLIAM J., JR. 1941—Notes on some mammals of Lee County, Florida. Amer. Midl. Nat. 25(3):686-691.

——— 1943—The mammals of eastern United States. Comstock, Ithaca.

HANDLEY, CHARLES O., AND CLYDE P. PATTON 1947—Wild mammals of Virginia. Comm. Game and Inland Fisheries, Richmond.

HARPER, FRANCIS 1927—The mammals of the Okefinokee Swamp region of Georgia. Proc. Boston Soc. Nat. Hist. 38(7):191-395.

HESSE, RICHARD, W. C. ALLEE, AND K. P. SCHMIDT 1937—Ecological animal geography. New York: John Wiley and Sons.

HILL, JOHN ERIC 1935—The cranial foramina in rodents. J. Mamm. 16(2):121-129.

HOWELL, ARTHUR H. 1919—Notes on the fox squirrels of the southeastern United States, with a description of a new form from Florida. Ibid. 1(1):36-38.

——— 1921—A biological survey of Alabama. North American Fauna No. 45.

LOWERY, GEORGE H., AND WILLIAM B. DAVIS 1942—A revision of the fox squirrels of the lower Mississippi Valley and Texas. Occas. Papers Mus. Zool., Louisiana State Univ., 9:153-172.

MOORE, JOSEPH C. 1946—Mammals from Welaka, Putnam County, Florida. J. Mamm. 27(1):49-59.

——— 1954—Fox squirrel receptionists. Everglades Nat. Hist., 2(2):152-160.

RIDGWAY, ROBERT 1912—Color standards and color nomenclature. Washington, D. C.

SETZER, HENRY W. 1949—Subspeciation in the kangaroo rat, *Dipodomys ordii*. Univ. Kansas Publs., Mus. Nat. Hist., 1(23):473-573.

SIMPSON, GEORGE GAYLORD 1929—The extinct land mammals of Florida. 20th Ann. Rept. Florida Geol. Surv. 229-280.

The Natural History of a Summer Aggregation of the Big Brown Bat, Eptesicus fuscus fuscus

John J. Christian[1]
Naval Medical Research Institute, Bethesda, Maryland

There is a surprising paucity of detailed information concerning *Eptesicus fuscus* in the eastern United States, although a few colonies have been studied in some detail in the West Coast. In contrast *Myotis* has been studied in great detail by a number of authors. The reproductive cycle of *Eptesicus* closely parallels that of *Myotis* with a few important exceptions, and will be discussed below.

Material and Methods

Dr. J. K. Doutt kindly provided the field data for 146 *Eptesicus fuscus* collected by the Pennsylvania Mammal Survey between 1946 and 1950. This material was used primarily in plotting the growth curve, but the available reproductive data were also used. Fifty-two female and 26 male *Eptesicus* collected during the warmer months of 1951, 1952 and 1953 in Washington Grove, Montgomery County, Maryland, were the source of all histologic, dental, and most life history data.

The Maryland bats were killed with chloroform, weighed and measured. After skinning and removing the skull, the carcass was placed in 10 percent neutral formalin with all viscera well exposed. Gross reproductive condition was noted and the testes measured prior to fixation. Adrenal weights were obtained after fixation. The gonads and adrenal glands of 69 bats were serially sectioned at 7 micra, and stained routinely with haematoxylin and eosin. The other viscera were sectioned in 14 animals. Mr. Herbert G. Ward provided assistance in preparing the histologic material.

After cleaning, anterior and lateral photographs of the skulls were taken by Dr. Merrill Wheatcroft of the Dental Division, Naval Medical Research Institute. I also owe Dr. Wheatcroft my thanks for advice and assistance on the problem of tooth wear in these bats.

Observations

The colony.—Washington Grove, Maryland, is in an old oak woods at an elevation of 625 feet. The tree canopy is dense, but the understory is a cleared park. The houses are frame structures, usually with wooden slatted shutters. These shutters, primarily on the second story, are the roosting places for summer aggregates of *Eptesicus fuscus*. Although there is a fair amount of movement from house to house following disturbances, certain shutters seem to serve as semipermanent annual roosts for individual colonies. In early summer these are nursery colonies composed of females and young. Males begin to

[1] The opinions or assertions contained herein are the private ones of the writer and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large.

appear late in July or early August, when the nursery colonies begin to break up. By September and October the sexes are mixed and the colonies broken into small groups. Prior to this time the males are solitary or in twos and threes. They apparently have no definite roost, seldom being found behind one shutter more than a night or two.

The roost of the principal observed colony was behind a second floor shutter on a south-facing wall. A solitary female on May 5, 1953 was the earliest arrival of a bat behind this shutter, although individuals were collected behind other shutters as early as April 3. The earliest first appearance of the colony was on June 25, 1951, when about 50 females and young took up their abode there. Five females, three lactating and two post-lactational, and two young were captured at this time. The colony left after being disturbed, but returned again on July 14. At this time the young were all flying, and the entire group was estimated to number between 30 and 35. The colony again departed on July 21. Single *Eptesicus* females with badly worn teeth or males were found from time to time behind various other shutters. None of the solitary females collected after June 1 was less than two years old (in their third summer), as indicated by their tooth wear (cf. below). There is no obvious explanation for this rather provocative fact, since gross and microscopic evidence indicated no reproductive failures.

On the 28th of July, 20 *Eptesicus* appeared behind a shutter on the north side of the house, stayed four nights, and departed following capture of several individuals. Presumably these were the same animals which had formed the original colony, but this is not certain. From this date on, the colony appears to have broken up, and no more than 3 or 4 were seen at a time behind any of several shutters.

Anticipating the 1952 arrival of the colony, the shutters were checked daily, beginning in mid-spring. The bats were absent through the morning of June 10, but during a very violent thunderstorm they were seen emerging from a hole about 40 feet above the ground in an oak trunk, whence they flew to the same shutter which had harbored the colony the preceding year. The number of full grown bats was estimated at 50. Five adult females, one pregnant and four nursing each a pair of small bats, were captured. One newborn young was gathered from the roof beneath the shutter. Since it was hoped that sampling at frequent intervals would provide complete data on growth, tooth development, and reproductive cycle, no more were collected at this time. Unfortunately, the colony returned to the oak tree the following day, where subsequently they were seen flying about the opening of the tree at dusk or after bad storms. In the meantime, solitary males were occasionally found behind various shutters. The morning of July 6 the entire colony had returned to the shutter and none was again around the oak tree. Thirteen young of the year and eight mature females were collected on July 7. One of the females was lactating, six were recently post-lactational, and the eighth was reproductively inactive. All but this last had an implantation scar in each cornu of the uterus. The colony at this time consisted of 75 to 80 bats, since very close to every fourth bat emerging from the shutter was collected. Following this disturbance the bats failed to return for the rest of the summer, although others were found in small groups and col-

lected on other houses up to October 27. Immediately following the July 7 collection, another colony was established behind a shutter on a house nearby. These may possibly have been the same animals that were driven away from the original colony.

Since the movements of these bats between the oak tree and the house had been witnessed once, and with evidence for its occurrence a second time, it is probable that we are dealing with the same group of bats up to July 7. This information offers a possible explanation for the relatively late appearance of the colony behind the shutter in both years. It seems likely that the young are born and raised to flight age in a warm, very sheltered spot such as the hollow oak tree. Then when the young are able to fly they leave this spot for a more accessible location, such as the shutters. This would appear to be the only logical explanation for not finding bats pregnant or nursing very young animals under ordinary circumstances, in spite of regular examinations of all shutters on a number of houses. On May 5, 1953 a solitary mature female containing two 6 mm embryos was collected from behind the same shutter.

In summary, it seems likely that female *Eptesicus* form maternity colonies in sheltered places such as hollow trees or chimneys. In a few weeks, when the young are beginning to fly, the colony moves to less sheltered quarters, in this case behind shutters which were relatively dry and shaded. When the young are approaching adult size in late July, the colony splits into smaller somewhat nomadic groups of mixed sex. With the advent of colder weather in mid-October *Eptesicus* have stored away large quantities of fat and are extremely lethargic or even torpid, hanging in groups of from 4 to 10 animals. None has been found after October 27; so it is presumed that they hibernate about this time.

Tooth wear as an age criterion.—The use of tooth wear to age bats has been largely neglected despite references attesting to its occurrence. Guthrie (1933) and Guthrie and Jeffers (1938) made no precise quantitative use of the degrees of tooth wear in *Myotis* and other species, although they divided *Myotis* into groups with no wear, some wear, and conspicuous wear (Guthrie, 1933). They could not have separated productive from nonproductive females in their first year on this basis. Pearson, Koford, and Pearson (1952) found no adequate dental criteria for aging in *Corynorhinus rafinesque*.

Marked variations in the degree of tooth wear were noted in the Maryland *Eptesicus*. Since the young of *Eptesicus* are born at approximately the same time each year, it seemed that tooth wear should occur in well-defined annual increments which could serve as a means of aging bats, as predicted by Laws (1952). In order to test this and to make sufficiently accurate measurements, anterior and lateral photographs were made of the skulls of 43 *Eptesicus* collected in June and July (Plates 1, 2). Only 39 of these bats had fully erupted dentition. The final prints gave a magnification of 6.3 times, determined by comparing the actual and photographic lengths of the maxillary tooth row, thus in most cases photographic measurements could be used directly without applying a correction factor. All measurements were made with a bow compass and estimated to the nearest tenth of a millimeter. It is these photographic measurements which will be referred to below.

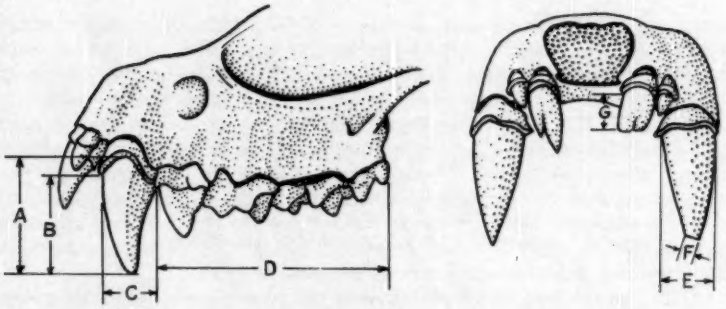


Fig. 1.—Measurements taken from photographs of *Eptesicus* skulls. A, lateral canine length; B, lateral anterior canine length; C, lateral canine base width; D, maxillary tooth row length; E, anterior canine base width; F, anterior canine occlusal tip width; G, anterior median incisor length.

Eight measurements were made for each skull, as shown in fig. 1. Plotting showed that three were sufficient: 1) the width of the upper canine occlusal tip, 2) the lateral anterior canine length from cingulum to occlusal tip, and 3) the median length of the median upper incisor from cingulum to occlusal tip. The two measurements made from the anterior view are the averages of the teeth on both sides. Molar wear was conspicuous (see Plates 1, 2), but proved difficult to measure from the photographs with consistent precision.

The frequency distribution of the anterior lateral upper canine lengths was plotted (fig. 2) and they fell into four distinct groups, the first of which

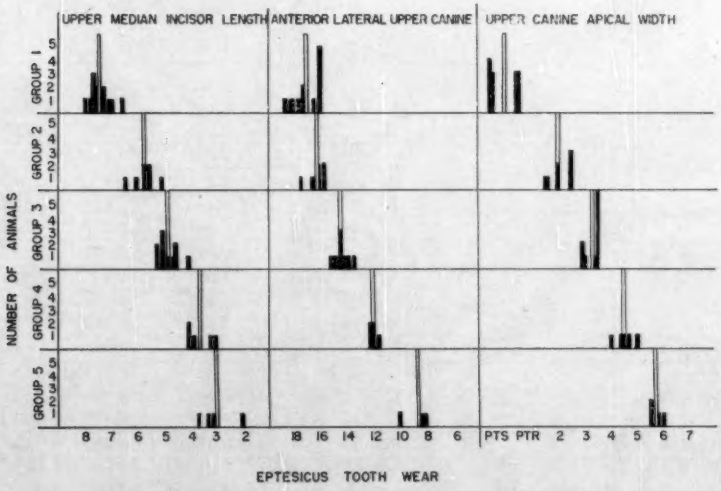


Fig. 2.—Frequency distribution of eptesicus tooth measurements (white=mean).

was quite broad. Examination of data on total length, body weight, uterine appearance, and stomach contents indicated that the first large group should be divided into two groups. The width of the upper canine apex and length of the upper median incisor proved to be excellent criteria for this subdivision (fig. 2; table 1). Table 1 summarizes the data on these three measurements, and shows the validity of separating the degrees of tooth wear into 5 distinct groups, plus a sixth group (0) for unerupted teeth. In each group, the three measurements are from the same individuals. Figure 2 and Table 1 indicate that the width of the upper canine occlusal surface gives the best separation into groups. In every case of overlap between groups of one measurement, the other two measurements provided adequate separation.

The bats captured in October showed wear between the June-July groups, which in each case was nearer the higher group. This follows since the prolonged annual hibernation of *Eptesicus* means that most feeding and tooth wear takes place from May to October. The tooth wear required to place the October animals in the next higher group would probably occur the following May and early June. The October specimens have been placed in the lower of the two bracketing tooth wear groups to put them in sequence with those of the same age class collected earlier in the summer.

For the balance of this paper group 0 includes young of the year with unerupted teeth; group 1 young of the year with fully erupted dentition;

TABLE 1.—Measurements on teeth of *Eptesicus*.

		No. bats per group	Median upper incisor length	Ant. lat. canine length	Upper canine apical width
		Mean	7.35	17.0	0.73
Group 1	13	S.D.	0.382	0.95	0.26
		S.E.	0.105	0.26	0.072
Group 1 vs. 2	P		0.001	0.1 -0.05	0.001
		Mean	5.7	16.3	2.01
Group 2	7	S.D.	0.438	0.667	0.397
		S.E.	0.164	0.252	0.145
Group 2 vs. 3	P		0.001	0.001	0.001
		Mean	4.80	14.4	3.33
Group 3	10	S.D.	0.437	0.596	0.275
		S.E.	0.138	0.189	0.087
Group 3 vs. 4	P		0.001	0.001	0.01
		Mean	3.60	12.0	4.5
Group 4	5	S.D.	0.469	0.20	0.717
		S.E.	0.21	0.179	0.321
Group 4 vs. 5	P		0.2	0.001	0.01
		Mean	3.03	8.70	5.7
Group 5	4	S.D.	0.728	0.673	0.245
		S.E.	0.364	0.336	0.122

and the subsequent groups are believed to represent 1 year increments; so that group 2 is one-year old, group 3 is two years old, etc.

Examination of cross sections of the teeth of these bats from various age groups reveals that the dentin is laid down in annular rings somewhat similar to those reported by Scheffer (1950) and Laws (1952) for seals. A wide band of dentin is deposited during the summer months followed by a dense zone during the period of hibernation (fig. 5). The annual layers also account for a recession of the pulp canal. These rings conform to the age based on

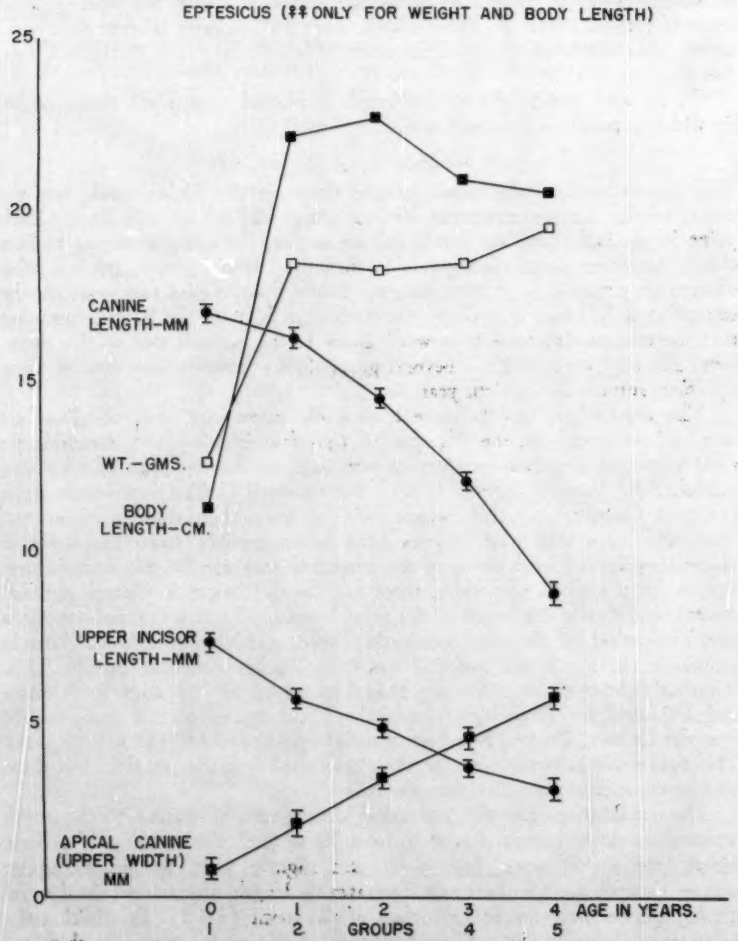


Fig. 3.—Mean canine length, upper incisor length, apical canine width, body weight, and body length plotted against tooth-wear group. Units of measurement are indicated. Horizontal cross bars are the standard errors of the mean tooth measurements for each group.

tooth wear and offer an exact method for aging this animal. Further work is in progress on the rings.

When the mean canine lengths are plotted against their respective groups (fig. 3), a curve is formed with increasing decrements of tooth wear between successive groups. If the occlusal canine width is similarly plotted (fig. 3) the relationship is a straight line with the increment constant between successive groups. The mean increment for occlusal tip and width is 1.22 mm (in reality 0.2 mm). The upper incisor length declines somewhat irregularly, but in general seems to decline in decreasing decrements with the wear greatest between groups 1 and 2. This follows, since the majority of first year wear occurs on a single thin cusp of the tooth (Plate 1, figs. 2, 4, 6; Plate 2, figs. 2, 4 ,6).

If, for each group, the canine length is plotted against the mean canine tip width, a parabola is formed with the formula

$$y = -0.262x^2 + 17.3 \text{ (fig. 4)}.$$

This curve describes the mean anterior shape of the canine tooth, but the means of the two measurements for any group will fall on this curve. Each point for an individual bat should fall on or near the curve according to how closely its canine shape corresponds to the mean. If the groups are indicative of age, i.e. group 2 = 1 year; etc., the points for the next two years can be extrapolated. When this is done, the sixth year falls on the X axis, meaning that the canines will have been worn down to the occlusal rim of the cingulum. No bats were captured beyond group 5; so probably very few of these *Eptesicus* survive to the sixth year.

The extrapolated points place a probable upper age limit of about six years (7 summers) on the life span of *Eptesicus* in Maryland, assuming no wear below the cingulum, conflicting with data on the life span of *Eptesicus* published by Banfield (1948, 1950). He reported banded individuals from Gatineau Company, Quebec, which survived more than eight years in two cases, and more than nine in one. One factor possibly accounting for this discrepancy is that wear down to the cingulum may not be the limit of usefulness for the tooth. Secondly, there may be differences in dietary abrasive content, and finally the length of the annual period of activity probably plays a role. The periods of *Eptesicus* activity in Quebec and Maryland should differ in proportion to the mean frost-free seasons. Figures provided by the U.S. Weather Bureau gave an average frost-free season of 148 days for Ottawa and 180 days for Frederick, Maryland. These figures give a probable life span for Ottawa, Quebec, based on Maryland figures of $180/148 \times = 7$ years. This figure still falls short of the three published longevity records, but these may be the exceptions rather than the rule.

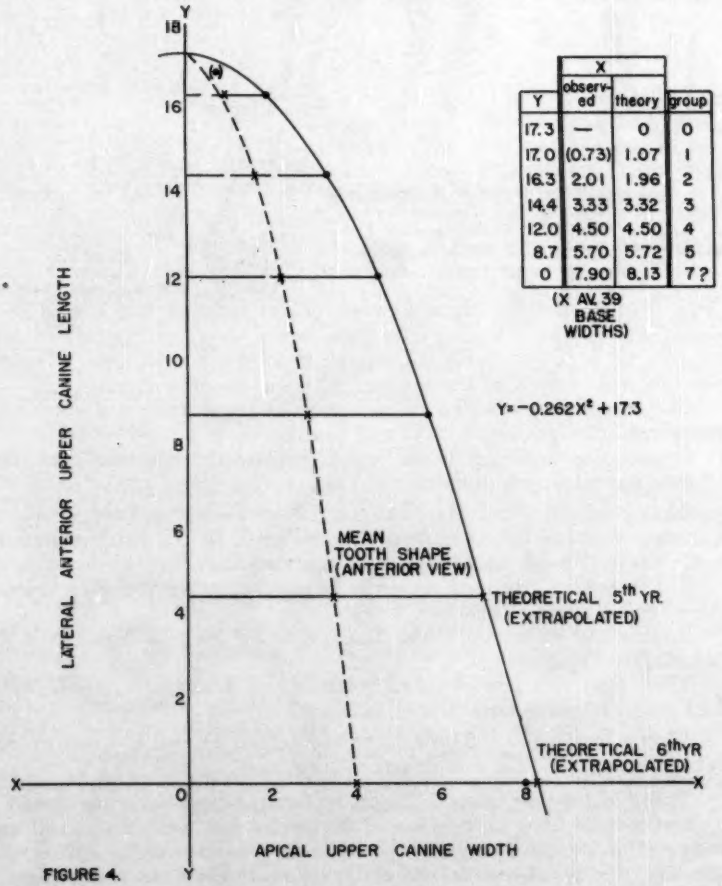
The explanation for the increasing decrements of canine tooth length between successive groups proved to be quite simple. Examination of ground sagittal sections of worn (group 4) and slightly worn (group 1) upper canines showed that as the tooth decreases in length, the enamel is abraded steadily thinner over the entire surface of the tooth (fig. 5). In addition the heavy enamel layer over the labial surface of the canine normally thins towards the base, and is actually quite thin over the anterior longitudinal groove. The lingual surface enamel is always quite thin. By the time the tooth has

worn to the late group 4 stage (October), the enamel has become extremely thin over the labial surface and absent over most of the lingual surface. There is also a simultaneous recession of the pulp canal by dentin deposition. Since the enamel is the most resistant, the length of the tooth decreases with increasing rapidity as the enamel becomes progressively thinner or absent. This basis for the increasingly greater tooth wear in *Eptesicus* canine teeth supports the belief that the groupings are essentially measures of time.

REPRODUCTION

FEMALES

The ovaries of 45 female *Eptesicus*, 15 in their first summer and 30 a year or more old were examined histologically. These will be grouped as



Y	X observed	X theory	group
17.3	—	0	0
17.0	(0.73)	1.07	1
16.3	2.01	1.96	2
14.4	3.33	3.32	3
12.0	4.50	4.50	4
8.7	5.70	5.72	5
0	7.90	8.13	7?

Fig. 4.—Eptesicus canine wear.

mature parous (and pregnant), and nulliparous and discussed under their dates of capture. The ovarian follicles and their modes of degeneration are classified according to Guthrie and Jeffers (1938): a primary follicle is a small, static peripheral follicle; a secondary follicle is a growing follicle with one or more layers in the granulosa, but with no antrum; and a tertiary follicle has a many-layered granulosa with an antrum. Type I degeneration is initiated by the cells of the granulosa and shows a conspicuous invasion by leucocytes in most cases, while Type II is atresia in which only the oöcyte degenerates and the granulosa remains intact.

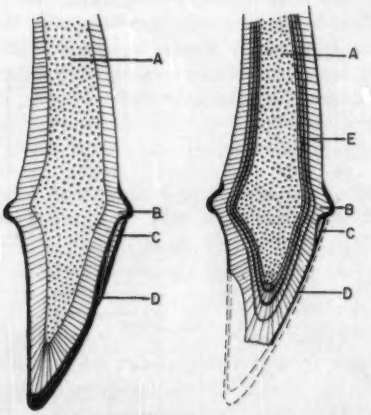


Fig. 5.—Longitudinal sections of a group 1 (left) and group 4 (right) Eptesicus teeth. A, pulp; B, dentin; C, anterior groove; D, enamel; E, layer of dense dentin deposition forming annual rings.

Mature females (April 3).—One female (group 3) had a single very large tertiary follicle in each ovary, the other from this date (group 2) had two of these follicles in one ovary and one in the other. All five of these follicles were as large or larger than the largest October follicles and each had a small thin-walled protuberance projecting into the lumen of the ovarian capsule-oviduct complex (Plate 6, figs. 3, 4), and were apparently close to the point of ovulation. All other follicles of any size were in various stages of atresia.

The interstitial cells were small with deeply staining nuclei and little finely vacuolated cytoplasm.

Spermatozoa were seen in the lateral portions of the uterine horns and adjacent quarter of each oviduct.

Mature female (April 6).—One group 2 female was captured which had a recently ruptured follicle in each ovary (Plate 6, fig. 5) and one ovum in each oviduct (Plate 6, fig. 6) along with shed cumulus cells.

The interstitial cells were decidedly larger than in the preceding animals due to increased cytoplasmic vacuolation.

Spermatozoa were found in the same portions of the genital tract as in the preceding two specimens.

These three bats provide strong evidence that ovulation occurs in Maryland *Eptesicus* during the first week in April.

Mature female (May 5).—One female (group 2) had a 6 mm embryo in each uterine horn. The ovaries were not examined.

Young of the year (June 10).—In four young females varying from 2.6 g (newborn) to 5.0 g in body weight the ovaries were exceedingly small and composed of a relatively wide peripheral band of ovarian cortex with 4 to 5 layers of primary oöcytes. In two of these females there was no distinguishable central mass of interstitial cells, but the other two (4.3, 5.0 g) had a

medulla half the width of the ovary with a few small unilaminar 2° follicles buried in it. These follicles were about twice the diameter of the 1° follicles around the periphery of the interstitial mass (Plate 4, fig. 3).

The interstitial cells were very small and undifferentiated with little cytoplasm and no visible vacuolation.

In two 7.0 g females the ovaries (Plate 4, fig. 4) were similar to the above except for an increase in size, primarily due to a medullary increase. There were still 4-5 rows of small primary follicles in the cortex. The number of unilaminar 2° follicles in the medulla was increased and the interstitial cells were undergoing active hyperplasia with abundant mitotic figures.

Parous females.—The ovaries of five females from groups 2, 3, 4 and 5 were histologically similar and will be treated as a group. One of these bats was pregnant with a near term 2.5 g embryo in each uterine horn. The other 4 were recently parturient, each with two nursing young. Four of these young weighed about 5 grams each, while the third pair weighed 7 g each.

The female with the 7 g young (Plate 5, fig. 4) had two tertiary follicles with very small antra, both in one ovary. None of the remaining follicles was beyond the trilaminar stage. No follicles in the pregnant or 3 nursing bats had developed beyond the early multilaminar stage (Plate 5, fig. 3). A corpus luteum was found in each ovary of the group. Most 2° follicles had large ova and one, two or three layers of granulosa cells. About half of these were undergoing type I degeneration. Secondary follicles were fewer than in immature females at the same stage of follicular development.

The ovarian interstitial and theca externa cells were uniformly large with abundant finely vacuolated cytoplasm. These cells were morphologically indistinguishable from those of the corpus luteum, the latter being distinguished primarily by deposits of blood pigment, the lack of an ovum, and a layer of compressed stromal cells around the periphery.

June 25.—No young females were captured. Two full-grown females were examined; one each from groups 2 and 3 (Plate 5, fig. 5).

These ovaries had a small number of 3° follicles with well formed antra, and a much larger number of large multilaminar 2° follicles approaching antrum formation. The interstitial cells were very large and well vacuolated, a single cell frequently containing four to six very large vacuoles.

Young of the year (July 7).—The ovaries of five females in their first summer, four in group 1 and one in group 0, were histologically similar (Plate 4, fig. 5). All had abundant 2° follicles up to large multilaminar in size, although the majority were bi- or trilaminar. As many as 19 of these latter follicles were counted in a single section. No very large multilaminar 2° or 3° follicles were seen. Polyovular follicles with up to 3 ova, most often 2, were frequently observed. None of the 2° follicles were retrogressing.

The interstitial cells were abundant and well vacuolated, and were responsible for the large gross size of the ovaries noted at this time.

Group 2 females.—The ovaries were examined of one female each from April 3, 6, 25, and June 10, two each from June 25 and July 7, (Plate 4, fig. 6) and one from July 13. Two of these were reproductively quiescent

with immature uteri and mammary glands, one had follicles about to rupture, one had tubal eggs, two were pregnant, and three were post-lactational. The ovaries of the productive group 2 bats were similar to the older bats for the same dates of capture, and are discussed under mature or parous females for their respective dates. Except for a lack of polyovular follicles and the presence of a number of 2° degenerating follicles the follicular development of the two nulliparous females was similar to young of the year for the same date (Plate 4, fig. 6). Follicular degeneration was usually type 1, but occasionally type 2 was noted.

The gross and microscopic evidence make it apparent that all female *Eptesicus fuscus* do not reproduce in their second summer. Whether the early April specimens would have been productive is not known, hence they are excluded from consideration at this point. These limited data suggest that perhaps three-quarters are productive at this age. The rate of follicular development in the ovaries of non-productive females is similar to that of young in their first summer on comparable dates, while productive individuals have the accelerated rate of older females, which are all parous, judging from the present material.

Parous females (7 animals; groups 2, 3 and 4).—This group included one lactating and six post-lactional bats. Each of these had one implantation scar in each uterine cornu. The ovaries were grossly enlarged.

Each ovary had numerous large multilaminar 2° follicles as well as earlier stages. About half of these follicles were degenerating, usually by type 1. One of these bats had no 3° follicles, but each ovary contained a single multilaminar 2° follicle nearing antrum formation which was much larger than the rest. The remaining ovaries each contained several large follicles in the stage of early antrum formation. In two pairs there was a single vesicular follicle much larger than the others in each ovary. No corpora lutea were found.

The interstitial cells were in general smaller than those of earlier mature bats or immature ovaries on the same date. The cytoplasm was reduced in proportion to the nucleus, was less well vacuolated, and stained more intensely with eosin.

July 13.—A single group 2 parous female was captured in which one uterine cornu was enlarged and the other juvenile in size.

One ovary (Plate 5, fig. 6) had 7 large 3° follicles of which 6 were degenerating. Nine of 11 follicles in the other ovary were degenerating, including all of the larger follicles. Numerous 2° follicles were in various stages of development.

The interstitial cells were still moderately vacuolated, but both the cell and vacuole size, as well as the number of vacuoles had decreased, compared to the July 7 animals. The vacuoles still were approximately equal in size; so that these cells had a fine foamy appearance.

July 18.—The ovaries of a single parous (group 3) female contained many 3° follicles (Plate 6, fig. 1). In one ovary there were two large 3° follicles with well developed antra, and another of this size was degenerating. In addition there were 12 smaller 3° follicles of which four were degenerating. Two

of seven 3° follicles, the same size as the two largest in the first ovary, were degenerating in the second ovary. No smaller 3° follicles were seen in this ovary. A third of the 2° follicles present were degenerating.

The interstitial cells were abundant, moderately large, and finely vacuolated, very similar to those of the July 13 females.

July 23.—One group 3 parous female was examined in which both ovaries had very large tertiary follicles with large antra and typical germ hillocks. In one ovary there were 5 of these plus a single degenerating 3° follicle. The other ovary contained one large 3° follicle and a second starting antrum formation. Secondary follicles were all small with bi- or trilaminar granulosa layers.

The interstitial cells were reduced in size and vacuole content as compared with the preceding animals.

Nulliparous young of the year (group 1) July 28-31.—Two females from this group had juvenile uteri, while the ovaries were enlarged and round. These ovaries contained many large multilaminar 2° follicles with half of them undergoing type I degeneration. A single triovular and numerous biovular follicles were found. One of these bats had three tertiary follicles of equal size with small antra in the only ovary examined (Plate 5, fig. 1). The other bat had five 3° follicles in each ovary with two in one ovary and one in the other which were half again as large as the rest.

The interstitial cells were smaller than on earlier dates, largely due to decrease in vacuole size. On close inspection the cells were found to be very finely vacuolated, but the cytoplasm appeared reduced and stained intensely as compared to late June and earlier July animals.

Parous females.—The ovaries from bats (groups 4 and 5) had numerous medium sized 2° follicles from tri- to multilaminar with half of them degenerating. In the group 4 bat one ovary had seven large 3° follicles with three of them degenerating, while the other ovary had 17 large 3° follicles with 12 of them in various stages of degeneration.

The interstitial cell mass appeared to consist entirely of large, well vacuolated theca externa cells which surrounded the larger follicles in broad bands. One ovary of the group 5 bat had five healthy appearing 3° follicles, one much larger than the others, plus four degenerating ones. The other ovary contained seven very large 3° follicles with six of them degenerating. The other ovary contained seven very large 3° follicles with six of them degenerating in addition to seven early 3° follicles, two of which were degenerate.

October 11.—The ovaries of the young of the year (group 1) were indistinguishable from those of older bats at this time, and will be treated as a single group. There was one bat from group 1, two from group 2, and one from group 4. The uterus of the group 1 bat was small and nulliparous, while the other three had typical parous uteri with enlarged cornua.

All of the ovaries contained many primary follicles and many large multilaminar 2° follicles with most of the latter degenerating (Type 1). All had 3° follicles with large well-developed antra (Plate 5, fig. 2). In the group 1 bat there were two large vesicular follicles in one ovary with a smaller third one degenerating. The other ovary had one large and three smaller degenerat-

ing tertiary follicles. Thus both maturing follicles were in the same ovary. A second bat (group 2) contained a single large vesicular follicle in each ovary (Plate 6, fig. 2). The other group 2 female had one large 3° follicle in one ovary, and two in the other without evidence of degeneration. The group 4 bat had two large 3° follicles in one ovary, and two, plus a degenerating one in the second ovary. One follicle in each ovary was conspicuously larger than the others.

The interstitial cells were small, intensely staining, and very finely vacuolated. They were similar to, but somewhat smaller than, those from the 31st of July.

October 27.—Three female *Eptesicus* were examined—two from group 1, and one from group 3. The ovaries were histologically similar in all three. The uterus of the group 1 animal was typically nulliparous, while the others were inactive parous uteri.

The ovaries had numerous large 2° follicles including multilaminar ones, but the majority were degenerating (type 1). Every ovary had one or more large 3° follicles. One bat had a single large 3° follicle in each ovary. The second had two large 3° follicles in one ovary and three in the other with one of the latter degenerating. The third *Eptesicus* had one large 3° follicle in one ovary and one normal plus two degenerate in the second ovary.

The interstitial cells were small with a large nucleus and little cytoplasm with little or no vacuolation. They were apparently completely quiescent.

Summary of ovarian development. Young of the year.—At birth the ovaries of *Eptesicus* are nothing but solid masses of primary oöcytes with the interstitial cells indistinguishable from undifferentiated fibroblasts. By the time the bats have attained a weight of 4.5 g a definite medulla has developed which contains a number of small-sized unilaminar 2° follicles. Ovarian growth continues and at a weight of 7.0 g there is an increase in the number of centrally located 2° follicles. Although the cortex still has four or five rows of primary oöcytes, its relative width is decreased. The 2° follicles continue to develop along with an increase in the interstitial cells; so that the ovary achieves essentially adult morphology by the end of July, when the animal is 12.0 g in weight. At this stage the number of secondary follicles is impressively greater than is seen in parous animals. Polyovular follicles are common and atresia of the 2° follicles is not noted.

By the end of July the young females have large multilaminar 2° follicles many of which are atretic. Polyovular follicles are still conspicuous.

The interstitial cells increase in size until they are large, well vacuolated cells by the first week in July. By the end of July these cells have decreased in size, due largely to a decrease in the intracytoplasmic vacuolation.

The ovaries of young *Eptesicus* captured on October 11 and 27 were indistinguishable from those of parous animals of the same date.

By early April the few surviving large follicles have formed a protrusion into the lumen of the oviduct-capsular complex, with marked thinning of the follicular wall over this protuberance. Rupture of the follicle and ovulation apparently soon follows, and tubal eggs were noted by the first week of April. All other large 2° or 3° follicles were atretic.

Females in their second summer (group 2).—The present data indicate that not all female *Eptesicus* are productive in the spring following their birth. The criteria of tooth wear and dentin rings have been used to age the animals, supported by their dates of capture and body weights. All had a total length greater than 118 mm and weight of 17.0 g or more as compared with a maximum of 116 mm and 15.0 g for known young of the year. Also nearly all of the young of the year had milk in their stomachs on the latest date of capture pertinent to this topic, when the group 2 animals were exclusively insectivorous.

Three-fourths of this group were pregnant or parous, and their ovaries were histologically similar to those of the older females. The nulliparous members showed a delayed early development of tertiary follicles and histological appearance similar to the young of the year except for a lack of polyovuly. Apparently pregnancy and/or lactation in some way accelerated follicular development, but not until after disappearance of the corpora lutea.

Parous female Eptesicus.—The ovaries show early antrum formation in a few follicles by June 10 in those bats with the oldest young, and which have lost their corpora lutea. At the same time bats which are pregnant or in early lactation have not lost their corpora lutea, and no follicles are found beyond the early multilaminar 2° stage. The interstitial cells are large and well vacuolated at this time.

By June 25 no corpora lutea are present, lactation has ceased in some females, and early tertiary follicles are found. The number of multilaminar secondary follicles has increased with no evidence of atresia at this time. The interstitial cells are extremely large and contain large vacuoles, suggesting cessation of activity.

Most parous females have well-developed 3° follicles by the first week in July, when lactation has almost ceased. About half of the 3° and more advanced 2° follicles are atretic, usually with invasion of the granulosa by leucocytes. The interstitial cells are decreasing in size by a diminution in the size of the vacuoles. No polyovular follicles were seen in the parous females.

Follicular development proceeds until the middle of July when a large number of 3° follicles have developed. Most of these are degenerative. Apparently there is rapid development of a large number of 3° follicles during July with most soon degenerating. Subsequently there is a reduced rate of degeneration until the October condition is attained.

After early October there are considerably fewer 3° follicles and most of the larger 2° or smaller 3° follicles are degenerating. The remaining 3° follicles were much larger than the largest July follicles. The total number of mature non-degenerating 3° follicles per bat varied from 2 to 4 in all groups. This is in contrast to Guthrie's (1933) finding seven follicles conspicuously larger than the others in one *Eptesicus* and six tubal eggs in another. The present data may indicate the usual number although the 7 October and 3 April animals examined is an admittedly small number. This tendency, however, is supported by the late July sample. In the nine females examined with fully developed nondegenerate 3° follicles the number of those distinctly larger than the others was as follows: two in seven bats, three three times, and four twice, suggesting that each female tends to mature two follicles annually.

This ovarian picture is essentially unchanged in early April, when ovulation occurs.

At this time the interstitial cells are small, with greatly shrunken cytoplasm, resulting largely from an almost complete loss of vacuolation.

MALES

The testes of 27 mature and immature male *Eptesicus fuscus* were examined between April 24 and October 27. Thirteen of these were young of the year.

Young of the year.—Two newborn 2.5 g males (June 10) had very small testes consisting of a few solid testis cords in a large mass of medium-sized, finely vacuolated interstitial cells. In contrast to the ovaries at this age, these interstitial cells were clearly differentiated and appear to be functional. The tubule sections contained a few resting spermatogonia and many undeveloped sertoli cells (Plate 3, fig. 1). These seminiferous cords were poorly convoluted and without lumens.

Three 4.5 to 4.8 g males from June 10 show a considerable increase in the size and convolutions of the seminiferous tubules, but they are still without lumens (Plate 3, fig. 2). Numerous mitotic figures were seen in the spermatogonial nuclei at this time. The interstitial cells were increased in size, primarily by an increase in cytoplasmic vacuolation. Two group 0 males captured June 25 weighed 8 and 10 grams. Their testes were essentially similar to those from June 10 except for further growth and convolution of the tubules. The interstitial cells were larger, but appeared somewhat decreased in number due to the tubular increase compared to the June 10 animals.

Six young males varying from 8.5 to 12.0 g on July 7 had testes 3.5 mm in length. Four of these with fully erupted canines were placed in group 1. The other two were in group 0. The seminiferous tubules were larger and more convoluted than those in the preceding group. Early lumen formation was evident in a few tubules, but the majority were still solid cords (Plate 3, fig. 3). There were many large resting primary spermatocytes and others in early stages of the first meiotic division. A very few leptotene primary spermatocytes were seen. Spermatogonial mitoses were still evident, but in much reduced numbers compared to the preceding animals.

Although still abundant, the interstitial cells showed a relative decrease in number from the June 25 bats, due primarily to the increase in tubule volume. The cells themselves were large and well vacuolated.

The seminiferous tubules of a young male (group 1) examined on July 31 were considerably larger than those of the July 7 males and had wide lumens (Plate 3, fig. 4). Every tubule contained primary spermatocytes which were either in the synizesis or pachytene stages of the first maturation division, although a very few still were in the leptotene stage. The interstitial cells were relatively reduced in numbers and were somewhat smaller than those in earlier specimens, due mainly to a reduction in the intracytoplasmic vacuolation.

By the 11th of October the testes of two young of the year (group 1) were indistinguishable from older bats captured at the same time. Spermatogenesis had ceased by mid-October. The seminiferous tubules still with patent lumens, were reduced in size and contained nothing but resting spermatogonia and

sertoli cells. A rare degenerate spermatozoan was seen free in the lumen of a tubule. The interstitial cells were small, unvacuolated, and reduced in number.

The tubules of the cauda epididymis of these males were packed with sperm, as in the older group. Spermiogenesis presumably occurs in late August and September.

From this evidence it appears that *Eptesicus* males reach sexual maturity during the summer of their birth. This contrasts with *Myotis* males which according to Miller (1939) do not reach maturity until their second summer.

Mature males (groups 2-5).—The testes of three male group 2 *Eptesicus* captured between April 24 and May 5 showed no evidence of activity. The tubules contained only Sertoli cells and resting spermatogonia. The tubular lumens, although patent, were greatly reduced in size. These seminiferous tubules showed essentially no change from the other specimen.

The interstititial cells showed a slight increase in vacuolization compared to the October specimens.

The epididymis contained sperm, but in reduced numbers compared to October.

Three males (groups 2, 3, and 4) captured June 19 and 22 were presumably in their second, third, and fourth summers. The testes, measuring 5.5 x 3 mm in one and 8 x 4.5 mm in the other two bats, were in an early stage of activity (Plate 3, fig. 5). Mitotic figures were abundant in the spermatogonia. Most tubules contained spermatocytes in an early stage of the first maturation division, while others were in the resting phase. The tubules were large, highly convoluted, and had small patent lumens. There was little interstitial tissue, clearly distinguishing these from immature testes. The interstitial cells had abundant finely vacuolated cytoplasm.

Proof of spermatogenic activity in the preceding summer was present in the group 2 bat: the cauda epididymis tubules, although greatly reduced in diameter, still had an occasional mass of very degenerate spermatozoa and leucocytes. Undischarged spermatozoa apparently became necrotic and are removed, at least in part, by dissolution and phagocytosis.

The testes of the only male examined on July 22 measured 11 x 6 mm. The tubules were large and there was relatively little interstitial tissue (Plate 3, fig. 6). The latter cells were reduced in size, owing to a considerable loss of cytoplasmic vacuolation as compared to the June bats. Spermatogenesis had proceeded to spermatids of Leblond and Clermont's stages 10 to 15 of spermiogenesis (1952). Spermatids in earlier stages of development and secondary spermatocytes were the commonest cells encountered. The number of primary spermatocytes located about the periphery of the tubules was reduced, most being in the pachytene stage of the first meiotic division.

The tubules of the cauda epididymis were large with wide lumens, but contained no spermatozoa.

Four adult males (groups 2, 3) were captured in October, three from the 11th and one from the 27th. These were alike and will be treated as a group. The testis dimensions at this time had regressed to an average 4.8 x 2.5 mm.

As in the young of the year for the same dates spermatogenesis had ceased in these males (Plate 4, fig. 2). The tubules, containing only peripherally

placed resting spermatogonia and sertoli cells, were reduced in diameter, although the lumens were still large. Occasional free, partially degenerate sperm cells were found in the lumens. The tubules of the cauda epididymis were large and filled with solid masses of spermatozoa (Plate 4, fig. 1).

Summary, mature males.—The development of mature *Eptesicus fuscus* testes so closely parallels that of *Myotis* (Miller, 1939) that a reconstruction of the annual spermatogenic cycle is warranted.

Although still reduced in size following winter inactivity, by the third week in June the tubules are undergoing rapid spermatogonial proliferation, many cells reaching the prochromosome stage of the primary spermatocyte. Tubular enlargement and spermatogenesis proceed until the tubules have reached full size by the 22nd of July, at which time spermatids are nearing maturity. Presumably this development continues until full scale spermiogenesis is reached in the early part of August. Mature *Eptesicus* reach full testicular activity considerably earlier than the young of the year, paralleling the time relationships for follicular development in young and mature females. Older males have maturing spermatids by the third week in July, whereas a week later the young of the year have not advanced beyond pachytene primary spermatocytes. The testes of the older animals, like the young of the year, retrogress during September, the seminiferous tubules having only spermatogonia and sertoli cells by the 11th of October. At this time the tubules of the cauda epididymis are packed with mature spermatozoa. The mean gross dimensions of October, April-May, and mid-June testes are similar.

The interstitial cells are maximally developed in June, and have decreased in cell and vacuole sizes by mid-July. Their cytoplasm decreases, primarily by a loss of vacuoles, until the cells appear little larger than the nuclei by mid-October. They probably remain in this condition until the following June.

The testes were located in the scrotal sacs in the youngest males examined, and appear to remain there throughout life.

ADRENAL CHANGES

Adrenal weights were recorded for all bats from the Maryland colony. These were standardized against the length of the head and body, expressed as milligrams per 100 millimeters of head and body length. This procedure is justified, since a linear relationship exists between length and adrenal weight for limited ranges of a species. This procedure was tested and resorted to, instead of using a body weight relationship, to avoid a false impression of adrenal atrophy resulting from pre-hibernation fat storage. In several October *Eptesicus* the subcutaneous body fat weighed between three and five grams per bat, or approximately 25% of the lean body weight.

Immature females, immature males, and all October bats of both sexes were statistically inseparable, having approximately the same combined adrenal weight/head and body length ratio. Thus all males and immature females, including the newborn of both sexes, have approximately the same relative adrenal mass with little variation throughout the summer and early fall months. The single pregnant and four lactating June 10 females show a significant ($P<0.01$) increase in relative and absolute adrenal weight. From this

time on there is a rapid and significant decline ($p<0.01$) to the July 7 post-lactational weight. Subsequently there is a gradual decline until October when mature females have the same adrenal weight as males and female young of the year. Figure 6 shows the mature and immature female mean adrenal weights with their standard errors, as well as the mean male adrenal weights for the period studied.

The increase in adrenal weight in pregnancy and lactation is due to a four-fold increase in the width of the cortical *zona fasciculata* brought about by cellular hypertrophy and hyperplasia. In all October *Eptesicus* and *fasciculata* is scarcely wider than the *zona glomerulosa*, and the reticularis is only a few cells wide. The cellular hypertrophy results primarily from a marked increase in the number and size of the cytoplasmic vacuoles of the zonae reticularis and fasciculata; so that the cells double their diameter in comparison to the October adrenals. The hyperplasia results in more than doubling the number of cells between the glomerulosa and the medulla in a single cortical cord. In these larger adrenals, there was no distinct demarcation between the zonae glomerulosa, fasciculata, and reticularis, the cells of all three zones being equal in size and vacuolation. As the adrenals lose weight, first the cells of the reticularis, followed by those of the fasciculata, lose lipid and the intracytoplasmic vacuoles become much smaller. The reticularis undergoes greater loss in this respect. The glomerulosa cells, however, retain or actually increase their lipid content; so that the demarcation between the zones soon becomes clear-cut.

It is evident that there is a pronounced adrenal cortical hypertrophy associated with pregnancy and early lactation, followed by a rapid decline so that the gland approaches its usual weight towards the end of lactation. There is

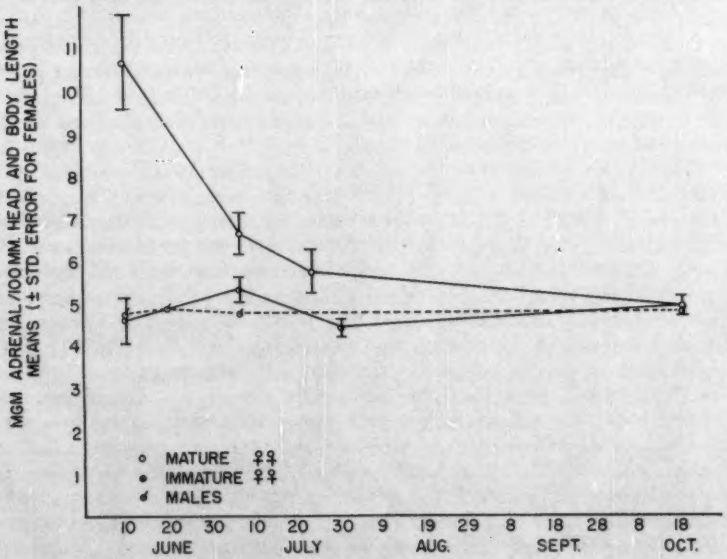


Fig. 6.—Eptesicus adrenal weight.

a parallel between the corpus luteum and adrenal cortical changes. The exact role the adrenal cortex plays in the reproductive process is still largely conjectural. It is generally believed that the adrenal cortices secrete sex steroids, and experimental evidence has pointed to the role of the adrenal cortex in maintaining placental circulatory integrity (Seifter, Christian, and Ehrich, 1951).

NUMBER OF YOUNG PER YEAR

A review of the literature reveals considerable conflicting evidence on the usual number of young in *Eptesicus*. Asdell (1946) states that all authorities agree that two is the usual number, but the number varies from one to four. Actually, however, this does not seem to be the case; since all authors writing of *Eptesicus* west of the Rocky Mts. give one as the usual number of young, and these reports are based on solid data. Howell (1919) states that Californian *Eptesicus* give birth to a single young during late May or early June. Howell and Little (1924) later state that about 3 dozen *Eptesicus* each had a single young varying from newborn to half grown. Borell and Ellis (1934) collected four pregnant *Eptesicus* in Nevada each with a single embryo, while Hall (1946) records fifteen pregnant females from the same state each with one embryo. Bailey (1931) makes the following statement about *Eptesicus* from New Mexico: ". . . the young, as shown by embryos and occasionally one clinging to the mother in flight, are apparently never more than one at birth." Bailey (1936) also reports four pregnant Oregon *Eptesicus* with a single embryo each on June 21, and on June 26 he obtained "a good series . . . all of which proved to be pregnant females carrying each a fully developed fetus." Finally Krutzsch (1946) noted that one young per female was usual in four colonies of *Eptesicus* from San Diego County, California, although he records a single instance of a female having 2 young. No other reports giving the number of young in western *Eptesicus* were found. These combined data, are convincing evidence, since with a single exception they give one as the number of young for *Eptesicus* in the far West.

This does not seem to be the case for eastern *Eptesicus*, although there is less published evidence. Harper (1929) records a female from Georgia with four young. Cahalane (1932) stated that three Michigan female *Eptesicus* each had one or two young clinging to her and a fourth gave birth to a single young. Guthrie (1933) reports a single specimen from Missouri with two young clinging to it, and two others with 4 and 6 tubal eggs respectively. Goodwin (1935) said that there are usually two in a litter in Connecticut, but that he believed the infant mortality was very high. Poole (1932) gives specific data on two Pennsylvanian *Eptesicus* each with two fetuses in utero. Female *Eptesicus* from Louisiana apparently average two young per year (Gates, 1937) since eleven bats had 23 young. One of these was known to have had three, another one, and three two each; the remaining seven had 16 young. Griffin (1940) states that *Eptesicus* in New England always seem to have two young per year, although he gives no specific data. Wimsatt (1945) contributed no additional information on the number of implantations or young born per female, but he counted 112 fertilized ova and 129 corpora lutea in 32 pregnant *Eptesicus* from Pennsylvania, or 3.5 fertilized ova per

bat. He assumes a litter size of one or two, based on the literature, and suggests that the symmetrically bicornuate uterus limits the litter size. Evidence presented in the preceding sections of this paper suggests that the ovary may play a part in this limitation, since the most frequent number of mature undegenerating Graafian follicles was two in the two ovaries.

There were data on reproduction for three *Eptesicus* from the Pennsylvania Mammal Survey. One of these had two young of 8.0 and 8.5 g clinging to her when captured on June 29, 1947. The other two females each had one right and one left uterine implantation scars. Data on reproduction was unavailable from the remainder of the specimens. In the material from Maryland one bat captured on June 25 had one right and no left implantation scar. A female collected May 5 contained 26 mm embryos. On July 7 seven female bats in which uterine implantation scars were found each had a scar in each uterine cornu. Five June 10 adult females, collected randomly from a colony of about 50, had two young apiece. One was pregnant with a near term fetus in each uterine horn, the other four had young clinging tightly to their nipples. Thus out of 17 bats in which the number of young or implantations was definitely known, 16 had two young each, while the remaining bat had one. The four bats with nursing young had uterine scars similar to those noted. Later in the year (late July through October) uterine scars were not grossly visible in any female; consequently it is believed that scars, when visible, represent young born not more than 2 or 3 weeks earlier. This belief is further supported by the fact that every bat with visible scars was either lactating or very recently post-lactational, and that five bats with two young apiece each had two uterine scars. It seems probable in the case of these *Eptesicus*, that the grossly visible uterine scars represent fairly accurately the number of young born as well as the number of implantations.

If 16 of 17 bats have two, and the 17th one young, the probability of there being two young is 0.942 with a standard deviation of $\pm$ 0.0567; so that the confidence limits at the 5% level are 0.829 and 1.055. One then can reasonably predict that at least 83% of productive eastern *Eptesicus* have two young a year apiece. These figures support previous accounts giving the usual number of young as two a year for *Eptesicus* in the U.S. east of the Rocky Mts. The evidence already cited for western *Eptesicus* having one a year leads to the conclusion that there is a fundamental difference in reproductive performance of *Eptesicus fuscus* in eastern and far western United States.

Goodwin's (1935) conclusion that the infant mortality of *Eptesicus* is high is not supported by the present study. The same colony from which 5 females with 10 young were collected on June 10 was again sampled on July 7. The shutter behind which the bats were roosting was agitated, and every fourth bat to emerge was collected; so that of a total number of 75-80, 21 were collected. Of these, 13 were young of the year, and eight were mature females, seven with two uterine scars each, and the eighth a reproductively quiescent group 2 female. The 13:7 ratio of young to productive females indicates a maximum loss of one of 14 possible, or 7% between birth and weaning. These figures, coupled with the October ratio of 1:1, suggest that mortality of the young is highest after weaning during their first summer. Goodwin's smaller Connecticut series of 10 two-week-old young and seven adult females

indicates a probable loss of 35%, based on the birthrate of 2 young per female per year.

GROWTH

Weight and total length data are available from 52 female and 27 male *Eptesicus* from Maryland and 146 *Eptesicus* from the Pennsylvania Mammal Survey. These data include bats of all ages captured in every month from March through October. For plotting the growth of *Eptesicus* all of these data were combined, since these bats conceive at the same time in Pennsylvania and Maryland and reach the same adult size. In any event, most of the data for infancy and early growth were gathered from the Maryland colony.

When the weights and lengths of the young are approaching mature size in the latter part of July, tooth-wear, reproductive data, and other pertinent observations were used to separate the young of the year from the older bats. Once mature weight and size is achieved, no attempt was made to separate these groups for plotting. The data for birth size was obtained from one 2.5 gm. young with attached umbilical cord and two embryos at term weighing 2.4 and 2.6 grams, figures which agree closely with those given by Poole (1932).

In order to include both length and weight data, the logarithm of the weight in grams times the total length in centimeters was plotted against time (fig. 7). Mature bats from June and July were placed in the second cycle of these months so there would be no confusion with the growth curve for the young of the year.

Inspection of the graph shows a rapid rate of growth from birth until the end of July, when there is a rapid decline in growth rate. By mid-August essentially adult weight and size is reached. There is little growth after this time, and toothwear groups, when available, show that differences are largely

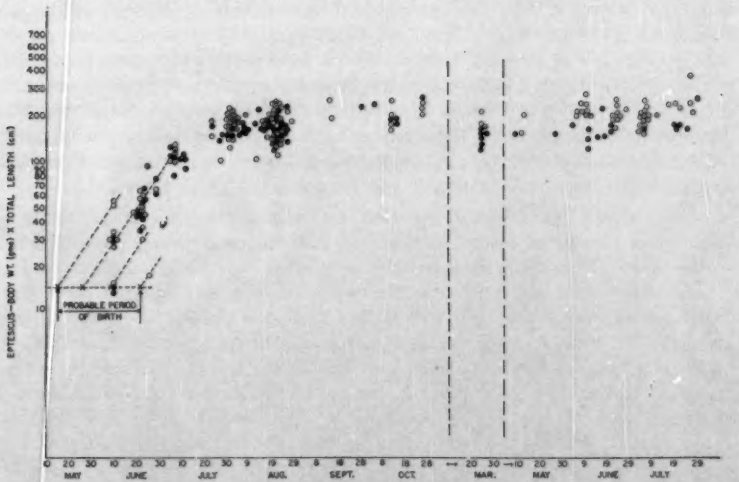


Fig. 7.—Eptesicus growth.

individual rather than on an age basis. Thus the growth of *Eptesicus* is not indefinite, as in the rodents.

Extrapolation of the growth curve shows that the majority of young are probably born between the 20th and 30th of May, but that the period of parturition probably extends from the second week in May to the end of the third week in June.

PARASITES

No detailed study was made of the diseases and parasites of these *Eptesicus*. The external parasites *Steatonyssus occidentalis* and *Cimex pilosellus* were identified, but these by no means comprise a complete list. An unidentified nematode was found deep in the gastric mucosa of several bats. Microscopic examinations of the intestinal contents of three bats were negative.

Of particular interest was Dr. Clay G. Huff's isolation and successful cultivation of trypanosomes from the heart blood of four of eight bats captured October 11. The adult forms of the trypanosomes were seen in the circulating blood and were also present in the cultures. These protozoa have not been completely identified or studied as yet, but additional work is in progress.

A purulent subcutaneous abscess was found on the foot of one bat, but no other abnormalities were found in a general survey of the tissues and organs of eight *Eptesicus*.

SUMMARY

Seventy-seven *Eptesicus fuscus* from a summer breeding aggregation in Maryland have been studied in detail with regard to the date of birth, number of young, reproductive cycle, wear and development of dentition and adrenal gland changes. Growth data was augmented by 146 individuals collected in Pennsylvania.

Ovulation occurs about the first week in April and the young are apparently born in hollow-tree maternity colonies, probably between May 15 and June 22. Their mean weight at birth is 2.5 g. The colony moves from the nursery to house shutters in late June or early July, where they remain until October with considerable shifting about and mixing of sexes after July. Most mature females cease lactating in the last week of June or first week of July. The young have flown, lost their deciduous teeth, and are weaned by this time. The young of the year reach nearly adult weight and length by the end of July, and in mid-August can be separated from older bats only by tooth wear.

It has been possible to age *Eptesicus* accurately by means of tooth wear, especially using the maxillary canines and incisors. The validity of age groups is further supported by the presence of annual growth rings of dentine and other data for the younger bats. The apical width plotted against the width fits the curve $y = -0.262X^2 + 17.3$. From these data was derived a probable mean maximum longevity of 6 years for Maryland *Eptesicus*. Differences in the length of frost-free seasons may account in part for the discrepancy for this figure and the 8 and 9 year figure for Quebec.

Canine wear occurs in increasing annual decrements, accounted for by a general thinning of the enamel with time in addition to a decrease in enamel width from apex to base in a young tooth.

The summer ovarian cycle has been described and summarized with the following salient points. The newborn bats have no differentiated ovarian interstitial tissue, but this rapidly develops along with the follicles, and follicular antra develop in the latter part of July. By October the ovaries of the young of the year have only a few large tertiary follicles remaining, most often two in the two ovaries, others having degenerated. Polyovular follicles were found in only the young of the year.

Parous females lose their corpora lutea by the time the young have reached 7.0 grams, and early antrum formation is detectable in the largest secondary follicles. This was found on June 10 in one animal, while most reached this stage by July 7. Accelerated follicle development and loss of corpora lutea apparently precedes the end of lactation. By mid-July large tertiary follicles are found in parous females. Development and regeneration of tertiary follicles proceeds throughout the summer and by the latter half of October the ovaries of parous females are identical to those of the young of the year.

The ovarian interstitial cells are large and well vacuolated at time of parturition, but soon start to decrease in size by loss of cytoplasmic vacuolation. By the end of lactation they are distinctly smaller and continue to decrease until October.

Some females in their second summer may not have borne young, and their follicular history parallels that of young of the year. Parous one-year-old females have the same ovarian sequence as older parous females.

The development of the testes parallels in time that of the ovaries. One outstanding feature is the presence at birth of well differentiated and vacuolated interstitial cells. From birth on there is a steady development of the testes, with early interstitial hyperplasia and continuous seminiferous tubule development. Full spermatogenesis is probably attained in mid-August.

Mature males in their second summer or older are distinguishable from young of the year by relatively less interstitial tissue in relation to the tubules. Spermiogenesis begins by the third week in July.

Spermatogenesis has ceased by mid-October in males of all ages. The testes contain only spermatogonia and sertoli cells, while the epipidymes are packed with mature spermatozoa. All male *Eptesicus* appear to reach reproductive maturity in their first summer.

Adrenal weights were obtained for all of the Maryland *Eptesicus*. Immature males and females, and mature males all have the same relative adrenal weight from early June through October. However, productive females have a twofold increase in relative adrenal weight during late pregnancy, followed by a very rapid decline to 30% greater than normal by the end of lactation, and then a gradual decline to the same weight as the other bats by October. The decrease in adrenal weight in parous females parallels the decline in size and vacuolation of the ovarian and testicular interstitial cells of both sexes with respect to time.

Two is the usual number of young in Maryland and Eastern *Eptesicus fuscus*, this number probably occurring in at least 83% of the female bats.

A survey of the literature has shown that *Eptesicus* from the far western states usually have one young a year.

Mortality prior to weaning is apparently not great, only 7% for the Maryland material.

An adult trypanosome was found in the blood stream of these bats, was successfully cultured, and maintained in culture in the adult form.

REFERENCES

ALLEN, G. M. 1939—Bats. Harvard Univ. Press, Cambridge.

ASDALL, S. A. 1946—Patterns of mammalian reproduction. Comstock Publ. Co., Ithaca.

BAILEY, V. 1931—Mammals of New Mexico. U. S. Biol. Surv., North Amer. Fauna 53:1-412.

——— 1936—Mammals and Life Zones of Oregon. Ibid. 55:1-416.

BANFIELD, A. W. F. 1948—Longevity of the big brown bat. J. Mamm. 29:418.

——— 1950—A further note on the longevity of the big brown bat. Ibid. 31:455.

BORELL, A. E. AND R. ELLIS 1934—Mammals of the Rocky Mountains region of northeastern Nevada. Ibid. 15:12-44.

CAHALANE, V. H. 1932—Large brown bat in Michigan. Ibid. 13:70-71.

GATES, W. H. 1937—Notes on the big brown bat. Ibid. 18:97-98.

GOODWIN, G. G. 1935—The Mammals of Connecticut. Conn. State Geol. Nat. Hist. Surv. Bull. 53:1-221.

GRIFFIN, D. R. 1940—Note on the life histories of New England Cave Bats. J. Mamm. 21:181-187.

GUTHRIE, M. J. 1933—The Reproductive Cycles of Some Cave Bats. Ibid. 14:199-216.

——— 1938—Growth of follicles in the ovaries of the bat Myotis lucifugus lucifugus. Anat. Rec. 71:477-496.

——— AND K. R. JEFFERS 1938—A cytological study of the ovaries of the bats Myotis lucifugus and Myotis grisescens. J. Morph. 62:528-557.

HALL, E. R. 1946—Mammals of Nevada. U. of Cal. Press, Berkeley. Pp. 151-153.

HARPER, F. 1929—Mammal notes from Randolph County, Georgia. J. Mamm. 10:84-85.

HOWELL, A. B. 1919—Some Californian experiences with bat roosts. Ibid. 1:169-177.

——— AND L. LITTLE 1924—Additional Notes on California bats with observations upon the Young of Eumops. Ibid. 5:261-263.

KRUTSCH, P. H. 1946—Some observations on the big brown bat in San Diego County, California. Ibid. 27:240-242.

LAWS, R. M. 1952—A new method of age determination for mammals. Nature 169: 972-973.

LEBLOND, C. P. AND CLERMONT 1952—Definition of the stages of the cycle of the seminiferous epithelium of the rat. Ann. N. Y. Acad. Sci. 55:548-573.

MILLER, R. E. 1939—The reproductive cycle in male bats of the species Myotis lucifugus lucifugus and Myotis grisescens. J. Morph. 64:267-295.

PEARSON, O. P., M. R. KOFORD AND A. K. PEARSON 1952—Reproduction of the lump-nosed bat (*Corynorhinus rafinesquii*) in California. J. Mamm. 33:273-320.

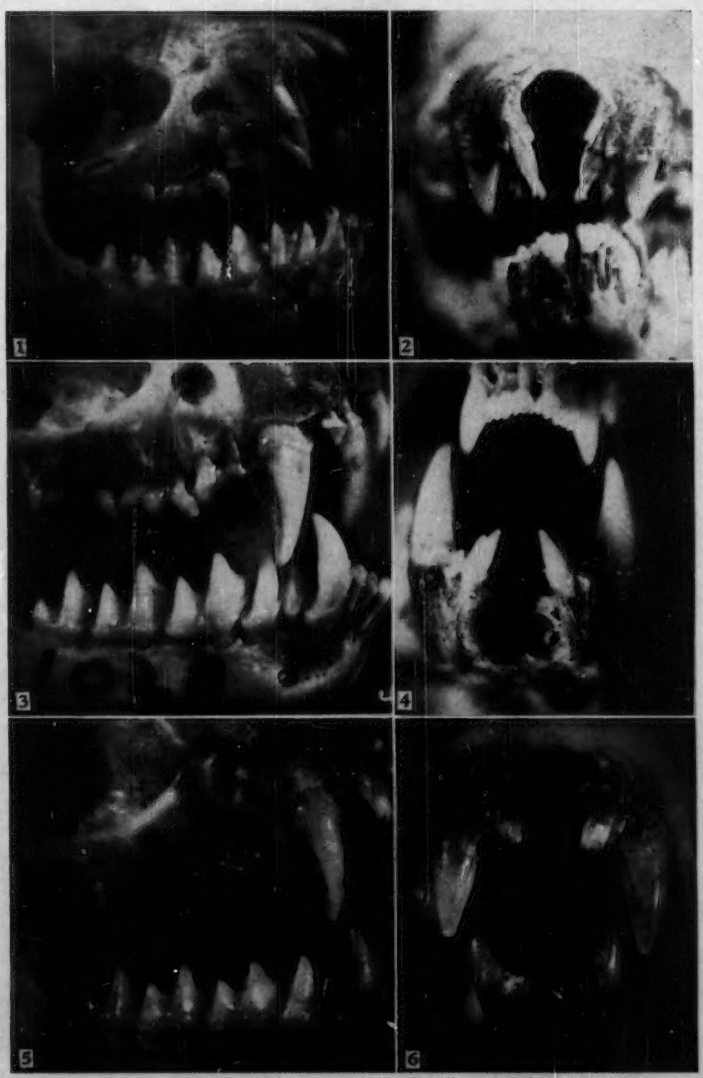
POOLE, E. L. 1932—A Survey of the Mammals of Berks County, Pennsylvania. Reading Publ. Mus. Art. Gall., Bull. No. 13.

SCHEFFER, V. B. 1950—Growth layers on the teeth of Pinnipedia as an indication of age. Science 112:309-311.

SEIFTER, J., J. J. CHRISTIAN AND W. E. EHRICH 1951—Effect of cortisone and other steroids on the hibernating gland of the pregnant white rat. Fed. Proc. 10:334.

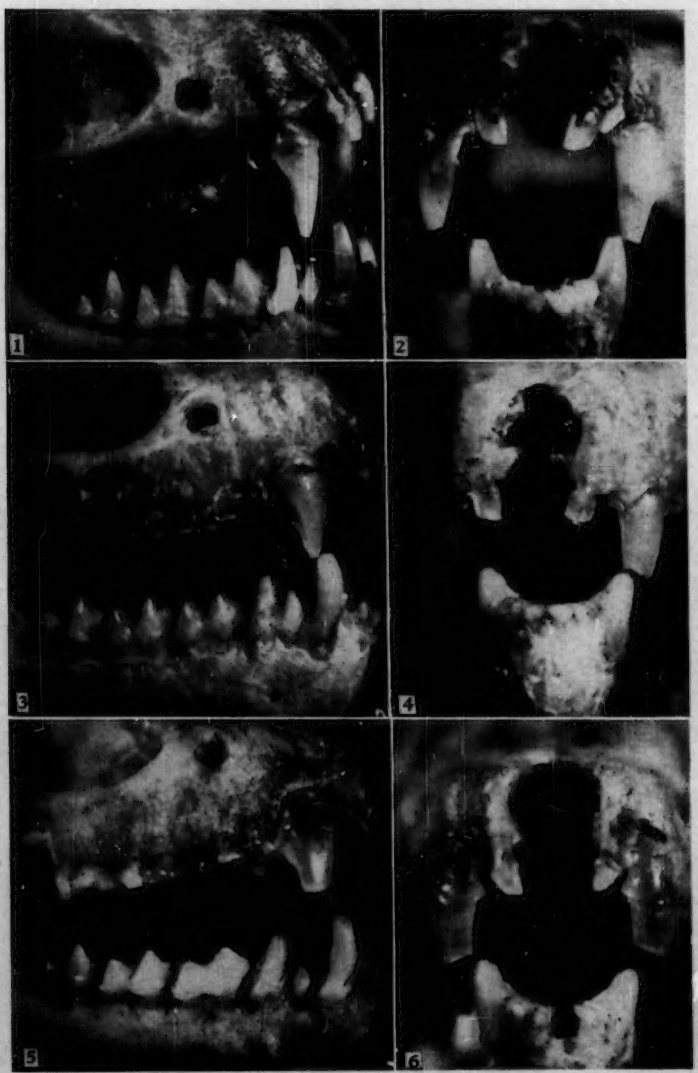
WIMSATT, W. A. 1945—Notes on breeding behavior, pregnancy and parturition in some vespertilionid bats of the Eastern United States. J. Mamm. 26:23-33.

PLATE 1



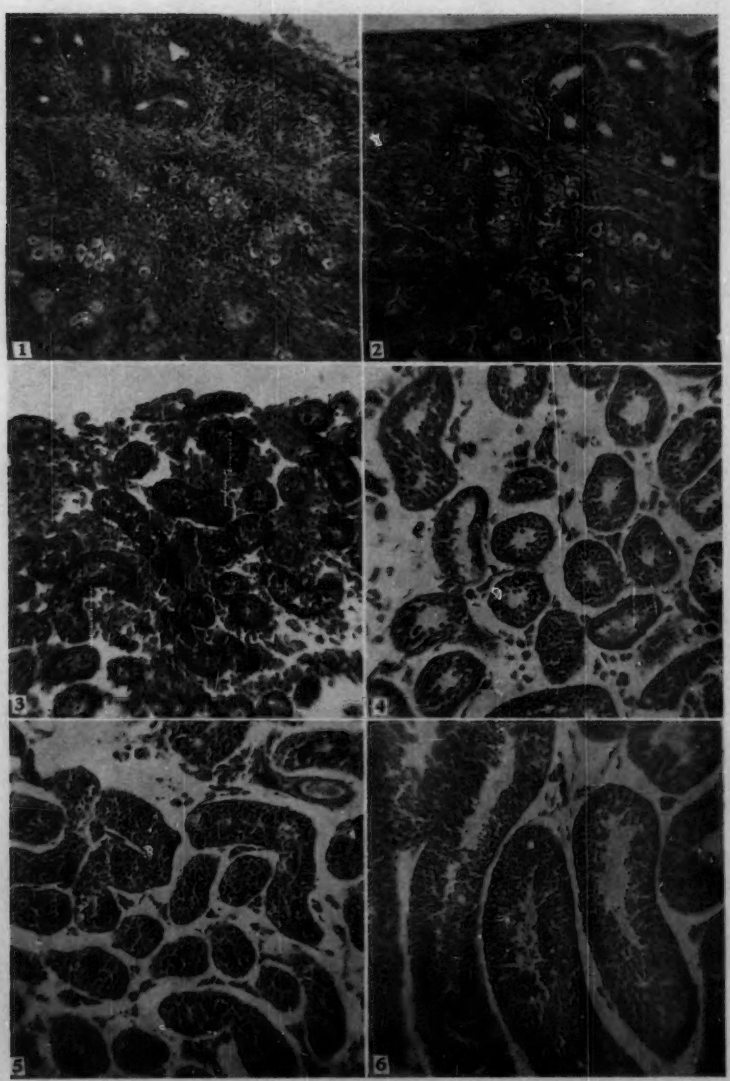
Figs. 1-6.—Lateral and anterior views of *Eptesicus* skulls arranged according to tooth wear group. 1, 2. Group O, showing deciduous teeth and unerupted canines; 3, 4. Group 1. Note sharp medial cusp of the upper incisors; 4, 5. Group 2. Note small increment of wear on canine, but marked wear on incisors.

PLATE 2



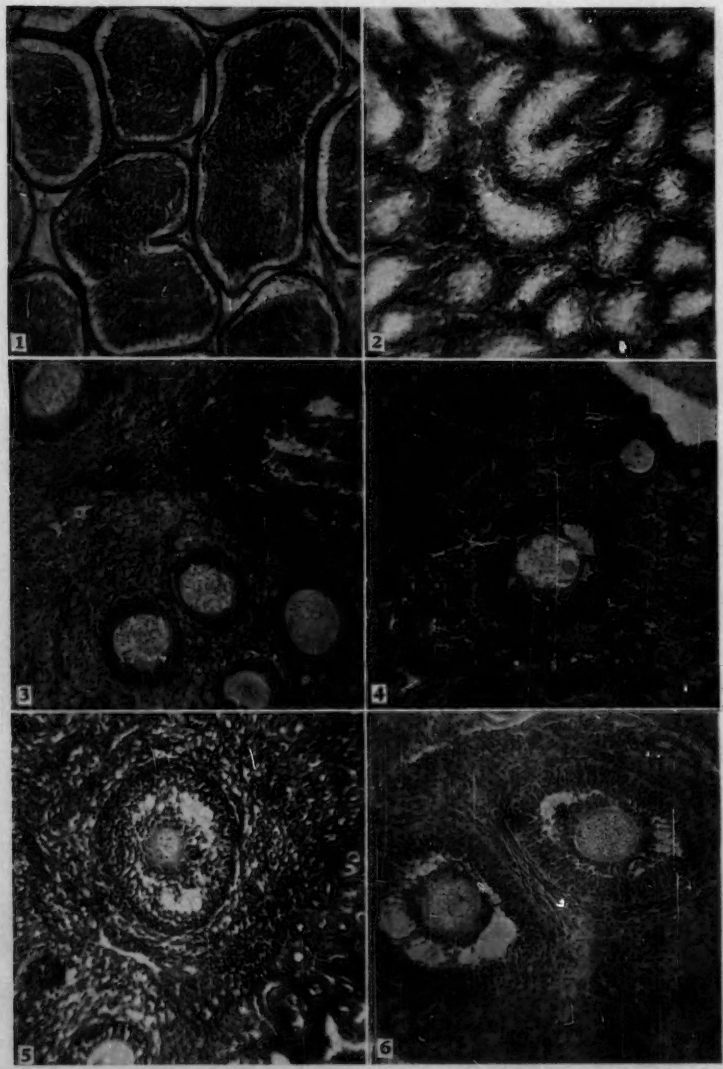
Figs. 1-6.—Lateral and anterior views of *Eptesicus* skulls arranged according to tooth wear group. 1, 2. Group 3; 3, 4. Group 4; 5, 6. Group 5.

PLATE 3



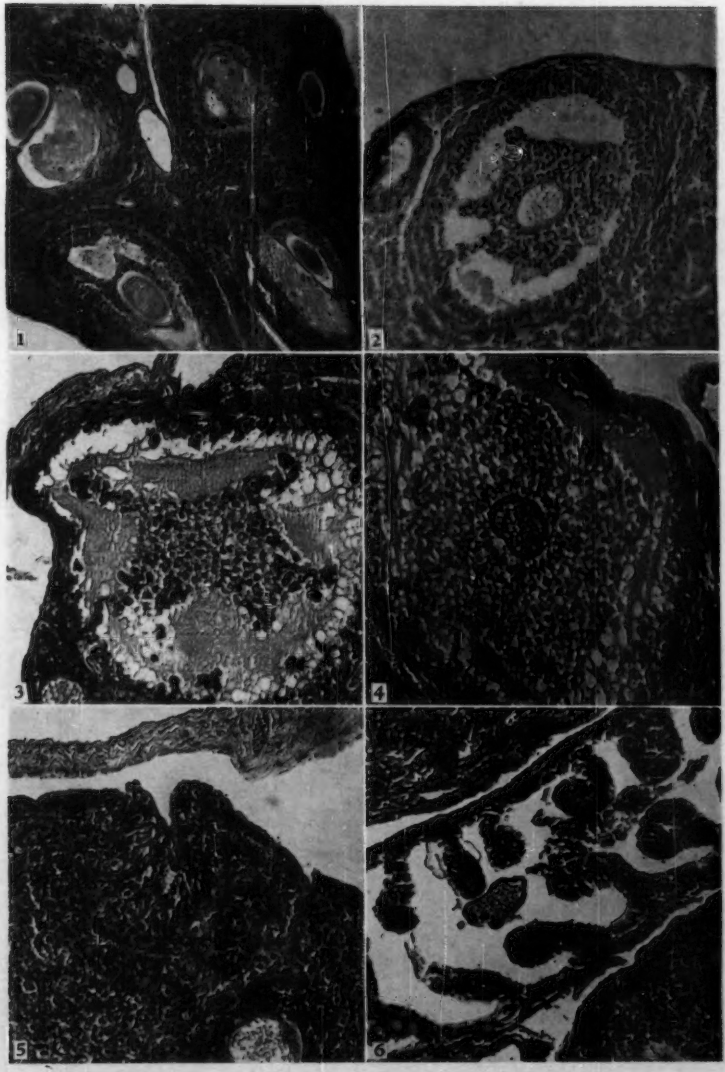
Figs. 1-6.—Sections of *Eptesicus* testes (x 100). 1. A 2.4 g young, captured June 10; 2. A 4.5 g young, captured June 10; 3. A group 1 11.1 g *Eptesicus;* 4. A 15 g group 1 bat captured July 31; 5. A 13.1 g group 2 male captured June 19; 6. A 15 g group 5 male captured July 22.

PLATE 4



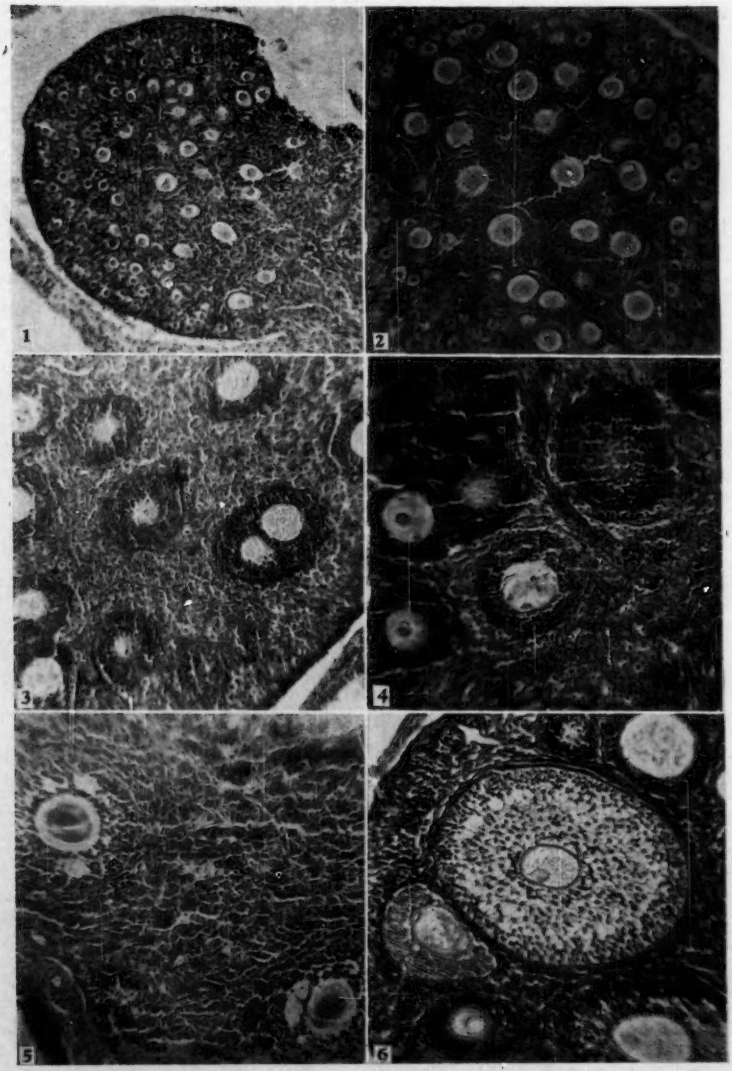
Figs. 1-6.—1. Epididymis of a group 3 Oct. 11 male showing tubules full of spermatozoa; 2. Testes tubules of a group 2 Oct. 11 male showing complete cessation of spermatogenesis. These two sections are typical of all males captured Oct. 11 and 25; 3. Ovary section of a group 4 female in late pregnancy captured June 10. Note large interstitial cells and follicles without autra; 4. Ovary of a group 3 lactating female *Eptesicus* with 2 7 gm young captured June 10. Note follicle with early antrum development; 5. Tertiary follicle in the ovary of a group 2 parous female *Eptesicus* captured June 25; 6. Two tertiary follicles in the ovary of a group 2 parous female captured July 13.

PLATE 5



Figs. 1-6.—1. Ovary of group 3 bat captured July 18. Three of four large tertiary follicles are degenerating; 2. Large tertiary follicle from a group 2 bat captured Oct. 11. This is typical of the October females; 3. A ripe ovarian follicle from a female captured April 3. This demonstrates very clearly the bulge into the lumen of the oviduct; 4. A similar follicle from another bat captured on the same date as 3; 5. A recently ruptured ovarian follicle from a group 2 bat captured April 6; 6. Oviduct containing an ovum from the same bat.

PLATE 6



Figs. 1-6.—1. Ovary of 4.3 g young female captured June 10; 2. Ovary of 7.6 g young female (group O) captured June 10; 3. Section of ovary of 12.6 g group O bat caught July 7. Note biovular follicle. 4. Largest follicles in ovary of 17.0 g group 2 nulliparous female captured July 7; 5. Early tertiary follicles in ovary of 16.0 g group 1 nulliparous female captured July 31; 6. Large tertiary follicle of 18.0 g group 1 female captured Oct. 11.

Foot-stirring as a feeding habit of Wood Ibis and Other Birds

A. L. Rand
Chicago Natural History Museum, Chicago, Illinois

When staying at the Archbold Biological Station, Lake Placid, Florida, in late June, 1954, I made some observations on a feeding habit of the wood ibis, *Mycteria americana* L. in which the feet are used and which seems to be unrecorded. In putting this on record I have correlated it with such related behavior in this and other species of birds as has come to my attention.

In the Wood Ibis

The feeding habit of the wood ibis most widely written about is the "muddying-the-water," in which the birds walk about in a shallow pond, stirring up the muddy bottom until the water is so muddy that fish and other aquatic animals come to the surface where the ibis kill them with a stroke of the bill. Not until a considerable number of animals are floating, dead, on the surface do the wood ibis eat them [an improbable delay when the birds are in flock as they usually are]. This was vividly described by Audubon (1835) and the description of this habit has been widely circulated, apparently usually paraphrased from Audubon when not quoted directly. Bent (1926) records seeing wood ibis feeling about in the mud with their bills for food; quotes an account of wood ibis walking back and forth in shallow water, dragging their bills beside them, pointed downward and backward and the birds opening and shutting their bills as though sifting the mud for food as do flamingoes; and quotes the above account from Audubon.

Bent gives stomach contents of California birds as fish, tadpoles, water beetles, paddle bugs, dragon fly larvae, water crickets, seeds and some vegetable matter. Howell (1932) records the stomach contents of Florida birds as mostly small-toothed minnows and some seeds. The birds are said to eat many other aquatic animals, including crabs, snakes, small turtles, frogs and even small mammals and young birds (Audubon). Probably they eat what is available. My observations indicated the Florida birds I saw were feeding chiefly on small items (insects? minnows?), but took large items when they appeared (a thick-bodied, twelve-inch snake).

My observations were made in the Lake Okeechobee area on four mornings in late June, 1954. The wood ibis were common locally in parties of from three to twenty birds, often in close proximity to other herons, especially the American Egret, *Egretta alba*, and the white ibis, *Guara alba*. They were by or in shallow ponds on the open grass prairie or on old cultivated, partly flooded fields. In the mornings the wood ibis fed actively until about eight o'clock, when most individuals left the ponds, walked a little distance onto dry land, and stood in groups or in lines resting for long periods. Only occasional birds were seen feeding later in the mornings. Observations were made from

a car on the highways, through seven power binoculars, and the birds were usually 100-200 yards away. Birds located at closer range usually stopped feeding and moved away.

The wood ibis when actively feeding walked back and forth across the small shallow ponds in the grass country, singly or in small parties. Periodically, sometimes at every step, more often at every second or third step, the bill was put down into the water, held there, and the bird, standing on one foot, brought the other foot up near its bill and moved the foot about in the water for a moment or two. Usually no catch was made, but occasionally a bird raised its bill, and made the characteristic jerking motion of its head that presumably moved a food item from its bill back into the mouth and swallowed it.

On some occasions the bill was seen to be open as it was put down. Most times this could not be ascertained. Many times at least the bill appeared to be put down until the tip touched the bottom of the pond. In a few cases the head was definitely under water. One got the impression that often the bird was balancing itself not only on one foot, but also on the tip of its bill as it moved its free foot near the bill. There was no stabbing, the bill was not moved about in the water, nor was it put down more than once at a place, and apparently there was little selection of the spot at which to put down the bill. The process appeared a random, periodic sampling in the line of march of the bird. Sometimes one foot, sometimes the other, was used in the stirring. Occasionally, and this was true especially of one bird feeding by itself, one wing, the one on the same side as the vibrated foot, was partly spread and moved. At first I wondered if this, too, was not part of an activity to startle prey into activity as has been recorded for the Louisiana Heron, but the spreading seemed to occur just before the bird moved on and I finally decided it had to do with the bird maintaining its balance.

Usually no food item could be seen in the bird's bill, indicating the bulk of the organisms caught were small.

The numerous apparent catches of food by the wood ibis contrasted with the few stabs at food made by the American Egrets that were feeding nearby, indicating the efficiency of the wood ibis' method of feeding in securing large numbers of items at least. That it was effective in satisfying the bird's hunger was evinced by most of them being satiated by eight o'clock.

Though this, the usual type of feeding I saw, had some of the elements of the "muddying the water" technique of Audubon, my interpretation is very different. It appeared that each bird was putting its bill down in the vegetation-filled water and then using one foot to "beat" through the vegetation and drive concealed small aquatic animals, probably insects, perhaps minnows, into its bill.

This adaptation seems an efficient, energy saving method on the part of a large bird that feeds on small active organisms; an alternative to a great deal of random searching and picking.

Though small items were usually taken, apparently this was not always so, for I saw one wood ibis with what appeared to be a thick-bodied snake some twelve inches long (method of capture not seen). It carried the twisting snake about for a few moments, pursued by four other wood ibis who were

apparently intent on taking it from the captor, and finally flew alone, with the snake far out on the prairie, where I lost sight of the bird.

Only rarely did I see a wood ibis apparently sight a prey item, walk a few steps to it and pick it up, but occasionally it happened as one would expect.

IN VARIOUS SPECIES

The use of their feet in a scratching, shuffling, vibrating or paddling motion by wading birds as an aid in getting food is known for some species, at least, in a number of groups: some herons (Ardeidae), the hammerhead stork (Scopidae), the wood ibis (Ciconiidae); some flamingoes (Phoenicopteridae); plover (Charadriidae), and gulls (Laridae).

Though the feet are moved about under water in connection with feeding by members of these diverse groups, the immediate aim seems to be different in some cases, correlated with the different methods of feeding. The main methods seem to be as follows:

(A) To cause worms to come to the surface by pattering the feet on wet turf, wet sand, or in shallow water. This seems to be employed chiefly by gulls, especially the herring gull (*Larus argentatus*), the common gull (*L. canus*), and the black-headed gull (*L. rudibundus*). The "treading" or "paddling" may resemble a dance of sorts, interrupted occasionally as a bird snatches up a worm, or only one foot may be used. It is considered by observers as an effective technique in bringing worms to the surface (Witherby, et al, 1941).

Possibly this method is also used by some small plover (*Charadrius*) (see under C).

(B) Stirring the water to cause food to float so that it is more easily accessible. This is the method of the flamingoes which feed with the top of their curiously twisted bill resting on the bottom and strain mud and water for the food items, small animals or plant material, contained. Apparently if the food is resting on a hard bottom, or in heavy mud it is relatively inaccessible. Ingraham (1896) writes of *Phoenicopterus ruber* that, "The water prevents their scratching like a fowl, but they go through the same motions, only not so fast, and as their long legs go up and down it reminds one of a regiment of soldiers marking time. After they have stirred up the earth for a while, they put their heads down into the water, [and] gather up the results of their labor. . . ." In feeding they swing around constantly gathering the earth into a mound.

Of the European form of this species it is recorded that the bird usually treads backwards (Witherby, et al, 1939), apparently so that the freshly treated area is immediately accessible to the bird without turning.

Young flamingoes in captivity do this same dancing or treading, especially easily observed when their food, hominy or rice, was put in a flat pan containing about two inches of water. "It being impossible for the birds to press the bill into the bottom of this receptacle, on entering it they at once "danced" and quickly caught the floating food." (Chapman, 1905). Mr. Karl Plath of the Chicago Zoological Society, Brookfield, Illinois, tells me that the adult flamingoes in the zoo regularly take food, ground shrimps and dried "flies" from the food container, drop it into the water, and indulge in "treading" while feeding on it there, indicating the rigid innateness of this behavior.

(C) The movement of the feet under some conditions to startle aquatic animals into activity so that they are more easily seen and caught is practiced by birds of several groups.

The three-banded plover (*Charadrius tricollaris*) has been recorded in Madagascar as stirring the water in front of it with one foot, and then pecking down apparently to seize some prey object thus brought to view (Milon, 1951). Somewhat similar actions or actions that more nearly recalled the paddling of gulls on wet sand, to bring worms to the surface have been described for several other small plover, but it has been pointed out that similar actions are also part of a display. Thus not all "paddling" or "treading" leg movements of plover are concerned with feeding.

A wading hammerhead stork (*Scopus umbretta*) in Southern Rhodesia has been seen to scratch the muddy bottom of a river, now with one foot, then with the other, and make a quick dab into it with its bill, and catch a crab or a small fish (Priest, 1933).

Certain species of herons also have this habit. McIlhenny (1936) describes as an unusual feeding method how snowy egrets (*Egretta thula*) and Louisiana herons (*Hydranassa tricolor*) slowly waded along in shallow water stretching one foot far in advance and vibrating it rapidly as the foot slid along the bottom apparently to frighten into activity small aquatic insects and minnows, so they could be seen and seized. This method was productive for McIlhenny observed that these birds made many more catches than did nearby American egrets (*Egretta alba*) and little blue herons (*Florida caerulea*) which did not use this foot movement. These observations were made in winter, and McIlhenny writes that it is only then, when the water is cold and prey inactive that such foot movements are used by the Louisiana herons.

(D) Stirring up the muddy bottom of pools to cause fish and other aquatic animals to come to the surface. This method, already mentioned above, is reminiscent of the "muddying the water" type of fishing done by negroes in the southeastern United States was described by Audubon (*loc. cit.*) for the wood ibis (*Mycteria americana*) and has been quoted a number of times as well as being observed by others since, apparently.

It would be interesting to have this checked by a modern observer.

(E) Holding the open bill in the water and driving aquatic insects out of hiding and into the bill. This method is described for the wood ibis, apparently for the first time, in the earlier part of this paper.

SUMMARY AND CONCLUSIONS

The method of feeding by the wood ibis, in which the bill is put in the water and one foot is moved through the vegetation-filled water to startle small aquatic animals out of hiding and into the bird's bill is described. Other feeding methods of the wood ibis are described. A brief review of the use of feet in feeding by other wading birds is given. Somewhat similar actions, scratching, "treading," paddling, shaking, shuffling, vibrating motions of the feet in the water, are known for members of six families.

Here we see quite diverse species that have evolved somewhat similar habits in a rather unusual direction. In one case at least the habit is shared by

two closely related species (snowy egret and Louisiana heron), but not by another, even more closely related species (snowy egret but not American egret). Apparently the habit originated independently a number of times.

Its function is toward economy of effort; instead of the bird moving its whole body, it moves only its slender appendages—its legs—and the method is apparently effective.

REFERENCES

AUDUBON, J. J. 1835—Ornithological biography, vol. III. Edinburgh.

BENT, A. C. 1926—Life histories of North American marsh birds. Bull. U. S. Nat. Mus., 135, pp. 1-490.

CHAPMAN, F. M. 1905—A Contribution to the life history of the American flamingo (*Phoenicopterus ruber*), with remarks upon specimens. Bull. Amer. Mus. Nat. Hist. 21, pp. 53-77.

HOWELL, A. H. 1932—Florida bird life. Florida Dept. of Game and Fresh Water Fish.

INGRAHAM, D. P. 1896—Observations on the American Flamingo, *Phoenicopterus ruber*, pp. 59-69. World's Congress on Ornithology. Chicago.

MCILHENNY, E. A. 1936—Unusual feeding habits of some of the Ardeidae. Auk 53, pp. 439-440.

MILON, PH. 1951—Notes D'Observation a Madagascar. IV. Vibration du pied sur les terrains de pâture et recouvrement des oeufs chez des Gravelots malgaches. Alauda 19:152-156.

PRIEST, C. D. 1933—The birds of Southern Rhodesia, vol. I. London.

WITHERBY, H. F., F. C. R. JOURDAIN, H. F. TICEHURST, AND B. W. TUCKER 1939—Handbook of British Birds, vols. III, V. London.

Growth and Development of the Green Frog, Rana clamitans, Under Natural Conditions[1]

Bernard Martof
University of Georgia, Athens

Compared to other vertebrates, relatively little is known concerning the rate of growth and development (other than embryonic) of amphibians in nature. In the laboratory, on the other hand, many physiological experiments, most of which concern the influence of endocrine secretions on the rate of growth and development of amphibians, have been reported. Noteworthy among these is the work of Swingle (1919, 1922) who studied the accelerating effect of thyroid extracts on metamorphosis. He found also that iodine or its inorganic compounds induced early transformation of amphibians. Many laboratory studies have been made of the rate of growth of amphibian larvae. In general, most of these studies, especially the more critical ones, deal with salamanders. Wilder (1924) pointed out that the curve representing the larval growth of *Eurycea bislineata* is sigmoid and Patch (1927) showed that two sigmoid curves are produced by *Ambystoma maculatum* and *A. tigrinum* as they increase in length, one curve being embryonic and the other larval. Later, Dempster (1930) found that the growth in weight of embryonic and larval *A. maculatum* under natural conditions may be expressed as a single sigmoid curve. Among the reports dealing with the growth of frog larvae are those of Davenport (1899) and Schaper (1902). They presented rather complete data on the larval growth in weight and volume of European species of *Rana* resulting from the acquisition of water, organic matter and ash. More recently, Burgess (1950) made a comparative study of the increase in body dimensions of larval *Scaphiopus hammondii,* some of which were reared in tap water and others in field-collected water.

With regard to the growth of transformed amphibians, only a few observations have been made. These are limited to the frogs and toads. Some data on the growth of *Rana pipiens* determined by study of length-frequency curves based on large numbers of individuals taken at the same time, have been presented by Force (1933). From recapture data obtained from 20 marked *Bufo terrestris,* Hamilton (1934) concluded that young toads double their length and are sexually mature by the time they are two years of age. Raney and Ingram (1941) found considerable variation in the rate of growth of *Rana catesbeiana,* reporting that the average bullfrog reaches sexual maturity in about a year following transformation and attains a size near the maximum during the subsequent year. Raney and Lachner (1947) reported that adult *Bufo terrestris* grow slowly and probably reach their maximum length in three or four years.

[1] This paper has been extracted from a dissertation submitted at the University of Michigan and done under the supervision of Frederick H. Test. It was expanded and prepared for publication while the author was at the University of Georgia. Accordingly, it is a contribution from both institutions.

In summary, many excellent laboratory studies have been made of the factors that influence growth and development of amphibians, but no major studies have been made of the way growth and development occur under the influence of the many and varying conditions of the natural habitat. It is hoped that the present report will add to the general understanding of these processes.

STUDY AREAS

This study was made during 1948 and 1949 on two study sites located near Ann Arbor, Michigan. One site, the Hogback area, was rectangular in shape, 15 acres in size, and consisted of a pastured field with three small ponds and a stream. The ponds were used as a breeding area by several species of frogs. A rather complete description of this area has been published in an earlier paper (Martof, 1953a). The other site, the Loch Alpin area, was somewhat L-shaped and extended over approximately 6.7 acres. It was restricted to the area actually occupied by green frogs in the vicinity of a clear, actively flowing stream. This study area has also been described in greater detail in another paper (Martof, 1953b). On both of these areas, the green frog was the most abundant amphibian.

GENERAL METHODS

The study sites were systematically and regularly visited so that a rather complete picture of growth and development could be obtained. Frogs were captured at all hours of the day and night and each was marked for future recognition by cutting the toes with scissors. Various combinations of cut digits indicated the serial number of the individual frogs. Units were indicated on the left hind foot, where a marked digit stood for number one, a marked second digit for number two, etc. For units larger than five, combinations of two toes, the fifth and another were used; e.g., the fifth and first toes were excised to denote number six, the fifth and second for number seven, etc. Tens were indicated similarly on the right hind foot and hundreds on the front feet. This plan permits a series of 6399 individuals to be marked, but the higher numbers were avoided by assigning a separate series of numbers to the frogs in each study area.

A snout-to-vent measurement of each specimen was made with vernier calipers. To be measured, a frog was held across the palm of the hand with one of its hind legs extending between the thumb and fore finger and its other leg extending between the fore and third fingers. The fourth and fifth fingers depressed the frog's back, making it extend to its full length. Calipers were then placed alongside the specimen, and while the fixed part of the calipers were supported by the fingers holding the frog and lined up with the anterior lip of the vent, the adjustable end of the calipers was moved to the tip of the snout. Frogs less than 50 mm in length were held on the fingers instead of the palm when measured. Readings were made to the nearest tenth of a millimeter.

A laboratory test of the accuracy of measurement indicated that with a frog about 65 mm in length the range of error was 0.6 mm. However, under varying field conditions this error was undoubtedly larger, increasing for larger frogs, poor lighting of late evening and early morning, precipitation, etc. Sometimes the error of measurement was so large as to annul completely the increment of

growth. However, in dealing with large numbers errors tend to average out.

Another measurement, the diameter of the tympanum, was taken from the anterior edge to the posterior edge of the left tympanic ring. Generally the tympana were nearly or quite round, but when the left one was otherwise, the right one was measured. If both were irregular in shape, as in 11 of the 2,018 frogs measured, then the average of the antero-posterior and dorso-ventral measurements of the more regular tympanum was used.

The sex of each adult frog was noted at the time of capture, the tympanum measurement proving useful for dubious cases, particularly for recently matured frogs. Data were also taken on the general physical condition—disease, injuries, scars, and other anomalous features. Because the nature and intensity of ventral markings and dorsal coloration varied considerably among individuals, general color patterns and markings were noted, thus providing a check on the identity of recaptured specimens.

Each frog was released at the place of capture, and information pertaining to the nature of the habitat was recorded (kind and density of vegetation, composition and wetness of the substratum, and distance from water). At no time were frogs removed from the areas and care was continuously exercised to preserve the naturalness of the study sites.

DATA COLLECTED

During 1948 and 1949, 1043 green frogs were marked on the Hogback area and 1221 at Loch Alpine. Of these 2264 frogs, one was captured fourteen times, one eleven times, and numerous others were taken less frequently to produce a total of 3402 captures (tables 1 and 2).

TABLE 1.—Frequency of capture of green frogs.

Area	Number of times an individual was captured											Total No. of frogs
	1	2	3	4	5	6	7	8	9	11	14	
Hogback	839	142	39	12	9	1	1					1043
L. Alpine	824	195	97	44	29	13	12	2	3	1	1	1221
Total	1663	337	136	56	38	14	13	2	3	1	1	2264

TABLE 2.—Number of captures of green frogs made annually at each area.

	Year		Total No. of captures
Area	1948	1949	
Hogback	339	1007	1346
L. Alpine	269	1787	2056
Total	608	2794	3402

GROWTH AND DEVELOPMENT

Length of Larval Life.—All reports in the literature indicate that in nature the green frog spends at least one winter in the larval stage, which lasts 370 to 400 days. A few suggest that occasionally two winters are passed as tadpoles.

Because of some fortunate events, evidence contrary to this was found. In 1948 the summer and fall were so dry that the ponds on the Hogback study area completely evaporated, killing myriads of tadpoles. The only frogs that completed their development that year were a small number of *R. pipiens* and *R. palustris*. The bottoms of the ponds were so thoroughly desiccated that deep clefts formed with the fracturing of the sun-baked soil, producing conditions which made it impossible for any tadpoles to survive there. By measuring the area and the average depth of the masses of dead and dying tadpoles in the last rapidly disappearing puddles and by counting the number of individuals in representative samples, it was estimated that 60,000-75,000 were present.

The next winter and spring the ponds were refilled. Then, in the summer and fall of 1949, a large number of newly transformed green frogs were taken in them. A mean estimate, determined from quadrat samples, indicated that on August 24 there were 10,700 newly transformed frogs present. Details of this population are given in another paper (Martof, in press).

It is highly improbable that so many tadpoles could have found their way into these ponds, which were connected by narrow canals through which they overflowed.

The easternmost pond overflowed into a stream and thus provided the only avenue by which tadpoles could move into the ponds. However, its characteristics would tend to prevent such movement because about twelve feet from the stream the water in the outlet passed downward into a muskrat burrow through which it entered the stream. A vertical descent of ten inches occurred at the place of entrance, providing an insurmountable barrier to tadpoles which might have been in the stream. At no time was the water observed to be high enough to permit tadpoles to get above this critical descent, although it is possible that such a level was attained early in the spring or immediately after late spring downpours. However, at such times the water was very swift and usually subsided in a few days. As tadpoles are weak swimmers and only eleven were collected in the stream in 1948 and five in 1949, it is unlikely that many, if any, got into the ponds from that source.

From the above data it seems conclusive that the larvae of *R. clamitans* may transform in the same season that the eggs are laid. I do not think that this early transformation is peculiar to this area alone; in fact, there is every reason to conclude that it is usual for eggs laid early in the spring. Eggs laid late in the breeding season, however, produced tadpoles that did not metamorphose until the following year. It is only because large numbers of such tadpoles were observed in the winter that previous authors thought over-wintering to be the usual event. Also it is only because of the circumstance of the drying of the ponds that there was opportunity to observe this feature of the life cycle. Similarly, in some newly constructed ponds in Iowa, Klimstra (1949) observed that the bullfrog required but one winter, instead of two as was formerly thought, for the completion of its larval development.

The first major breeding activity at Hogback in 1949 occurred on May 31

and on this date the first egg cluster of the season was found, although a few green frogs were calling in the ponds as early as May 5. In all probability eggs that were laid in the last half of May—very likely May 31—produced the transforming individuals observed during the second week of August. Therefore, the larval period is concluded to have been approximately 70-85 days, about the same as that of species of *Rana* that lay earlier in the season. The major difference is that the development of the green frog occurs at considerably higher temperatures.

Tadpoles that overwintered in the permanent lakes located just south of the study area at Loch Alpine were found transforming from June 5 to July 12, 1949. In this period only eight frogs with tail stubs, positive evidence of recent metamorphosis, were observed, in contrast to the large concentration of newly transformed frogs seen there later in the summer. From June 5 to July 12 the subadults, in spite of their great losses from the area as indicated by the lack of recaptures and the influx of unmarked frogs, composed about 50 percent of the total population on the whole area, suggesting that replacement as a result of metamorphosis was occurring (Martof, in press). The marked decline in percentage of subadults in the last half of July and the first week of August was caused to a large extent by the absence of newly transformed frogs. All overwintering tadpoles had transformed, and the current season's larvae had not yet developed sufficiently to metamorphose.

The length of time in the larval stage varied because of the prolonged breeding season. Eggs laid early in the season developed into frogs late in the same year, August 3 to September 28, while ova deposited later did not develop into frogs until June 5 to July 12 of the following year. These dates of metamorphosis indicate the periods during which frogs with portions of their larval tails were captured. The periods were the same on both study areas, perhaps indicating no major ecologic differences in the environments of the tadpoles. Thus the larval period may be 70-85 days or as long as 335-360 days. Because of this varying length of the larval period the age of newly transformed individuals differed considerably.

It is interesting that the breeding season of the green frog extended over about three months, from about mid-May to mid-August, and also that the period during which transforming frogs were taken had about the same duration, August 3 to September 28 and June 5 to July 12. From these data it appears that July 10 was near the critical time of egg laying; eggs deposited after this date did not develop into frogs until the following year. Because of the higher temperatures that occur earlier in the fall season of metamorphosis and the direct correlation of the number of males in the breeding ponds with the estimated number of newly transformed frogs later taken in these same ponds, it was thought that eggs laid before June 25 usually developed into frogs in the latter part of the same season. Thus tadpoles developed from eggs laid June 25 to July 10 may or may not metamorphose in the season, depending largely on weather conditions.

At Ithaca, New York, which has approximately the same latitude as Ann Arbor, Mich., Wright (1914) obtained similar figures for the length of the breeding season and for the annual period of activity of green frogs. But he observed that transformation usually started about June 28 and was largely

completed by the first of August, from which one might surmise that the temperatures in 1949 at Ann Arbor were higher than average and, in fact, they were. In May, June, and July the average daily temperatures were about four degrees F above the mean monthly temperatures. However, Wright (1932) thought that one entire year was the normal tadpole life for the green frog even in the southeastern part of the United States, where average annual temperatures are about 20 degrees F higher than at Ann Arbor and Ithaca.

It is possible that the temperature of the spring-fed ponds at Ithaca is considerably lower than that found here in stagnant water of open ponds. But on the other hand, Wright's data for the laying and transformation seasons of related species (*R. pipiens*, *R. palustris*, and *R. sylvatica*) at Ithaca are in perfect accord with my findings here at Ann Arbor. In view of this coincidence of data for related species, it is concluded that in the United States eggs of *R. clamitans* laid early in the year may produce frogs in the same season.

The results of Ting (1951) serve to confirm observations of the early transformation of green frogs. He artificially fertilized green frog eggs in the laboratory, and 92 days later some of the resulting larvae transformed.

Growth of Transformed Frogs.—In this report, growth is indicated by an increase in the length of transformed individuals as shown by their snout-to-vent measurements. The rate at which green frogs grow has never been accurately determined. Wright (1932) calculated that the smaller southern green frog added about 11 mm to its length every year for three or four years. Exclusive of the study by Raney and Ingram (1941) of the annual growth of four males, no other literature pertaining to growth was found. Indeed, at most only a few accurate measurements of green frogs are available. It is believed that the following data and analyses will throw some light on growth.

Many newly transformed frogs were captured from August 8 to September 15, 1949 in the breeding area at Hogback. As there was no resident population of green frogs and since the recently metamorphosed individuals generally departed from the ponds soon after their tail stubs were absorbed, there was no danger of confusing them with the older frogs. As a result, the mean body length at which they began their amphibious existence was readily obtained. The range in size of the 286 frogs measured was 28.4 to 36.3 mm with the mean at 32.6 mm. The largest frog in this range still had a part of its tail. Wright (1914) measured 41 specimens presumably overwintering at Ithaca, N. Y., in which the mean body length was 32 mm with a range of 28 to 38 mm, sizes almost identical for those obtained in the Ann Arbor area.

Occasional individuals doubtless transform at larger or smaller size than indicated by these figures. For example, at Loch Alpine, August 14, 1949, a frog, taken about 30 meters from a breeding pond, measured only 22.9 mm. It would be interesting to know the history of this diminutive frog. Disease and/or hereditary causes perhaps may be considered responsible but more likely it was trapped in a pond where crowding of tadpoles resulted. Adolph (1931) pointed out that crowded larvae did not feed as readily as uncrowded ones, even though an excess of food was available. He suggested that this resulted in a reduced growth rate. Lynn and Edelman (1936) showed that crowding not only caused slow growth but also later metamorphosis and high

mortality, which they concluded to be caused by oversimplification as a result of frequent contacts in crowded cultures.

The above record was the only one which did not coincide with the range given for newly transformed green frogs. However, Walker (1946) reported an exceptionally small Ohio frog, only 21 mm long. On the other hand, examples of gigantism as reported by Angel (1946), could be identified with certainty only while the larval tail was being resorbed.

Individuals that had wintered as tadpoles metamorphosed at the same average size as those that completed their larval development the same season the eggs were laid. Not enough data on the growth of individuals having different sizes at the completion of the tadpole stage were available to permit any correlations with the rate of later growth and final body length.

In order to learn the relative amount of growth occurring in different months, all records taken in 1949 of individuals that were 1) recaptured within a period of 45 days and 2) between 40 and 60 mm long at both captures, whatever the month, were selected. This size was chosen because growth was relatively and absolutely greater in comparison with that of larger frogs, and accordingly the percentage of error in measurement was smaller. There were only a few recaptures of frogs shorter than 40 mm, and it was thought that the data would be more significant if they were not included. With the group thus fairly uniform, the effects of size upon growth was largely obviated. To increase further the homogeneity of the group, records of seriously injured, diseased, or deformed frogs were discarded. These were not evenly distributed throughout the year, and most showed retarded growth. The above selected records were next grouped according to the calendar month in which most of the interval between captures occurred. Then the mean size of all frogs—as shown by their initial measurements, the average growth per day, and the average increase in length per thirty days were ascertained for each month (table 3).

The monthly data in table 3 are plotted in fig. 1 and clearly show the seasonal variation in growth. The shape of the growth curve is sigmoid. After hibernation, growth was resumed late in April or early in May. Throughout May it was accelerated becoming somewhat linear in June and July. During the latter part of August and the first half of September the growth rate de-

TABLE 3.—Monthly variation in growth of 40-60 mm green frogs in the Ann Arbor region. Measurements in millimeters.

Month	Number of records	Mean Size	Average growth per day	per 30 days	% of av. annual growth
April	8	48.6	.09	2.7	8.3
May	57	49.2	.18	5.4	16.7
June	71	48.0	.24	7.2	22.2
July	54	51.8	.29	8.7	26.9
August	54	49.4	.17	5.1	15.7
September	76	47.9	.08	2.4	7.4
October	34	47.6	.03	0.9	2.8

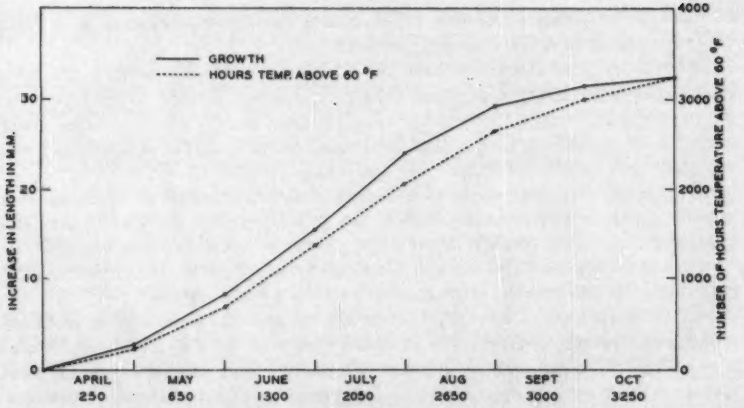


Fig. 1.—The correlation of growth with temperature as shown by a composite curve of the monthly growth for frogs of 40-60 mm length and the number of hours the temperature was above 60°F.

clined slowly. No definite increase in size was observed in the period from late October to April, in fact, a fraction of a millimeter of shrinkage was noted for most frogs. Occasional growth was indicated for this period but at no time did the increment of increase exceed the expected error of measurement. Consequently this decrease in size was perhaps the result of the fact that measurements were taken from the tip of the snout to the anterior lip of the cloacal aperture, rather than to a bony structure. Intrinsic changes preparing frogs for hibernation, as an increase in muscle tonus and a decrease in blood volume (Holzapfel, 1937), in addition to the absence of food and undigestible matter in the alimentary tract, especially the cloaca, may be responsible. It is clearly evident that the growing period is relatively short, being chiefly confined to about four months, mid-May to mid-September.

In order to get a direct picture of the season of growth for an individual, the records of about 400 of the most frequently captured frogs were plotted. Fig. 2, a typical example, shows some important characteristics of amphibian growth and closely resembles the composite curve of seasonal growth (fig. 1). The fundamental difference in these curves is that the composite one shows how growth varies through the season for frogs of approximately the same size, whereas the other curve indicates the growth of the same individual throughout the year.

The growth of plants and animals is known to be profoundly affected by two external factors, temperature and availability of food (Thompson, 1942). For the green frog, these are intimately related. Low temperatures not only cause green frogs, but also their chief food items—insects—to become inactive.

The close correlation of growth with temperature is clearly indicated in two ways. In fig. 3, the curve showing the percentage of growth accomplished each month is strikingly similar to that of the mean monthly temperatures. It should be pointed out that the temperature data are from the Willow Run

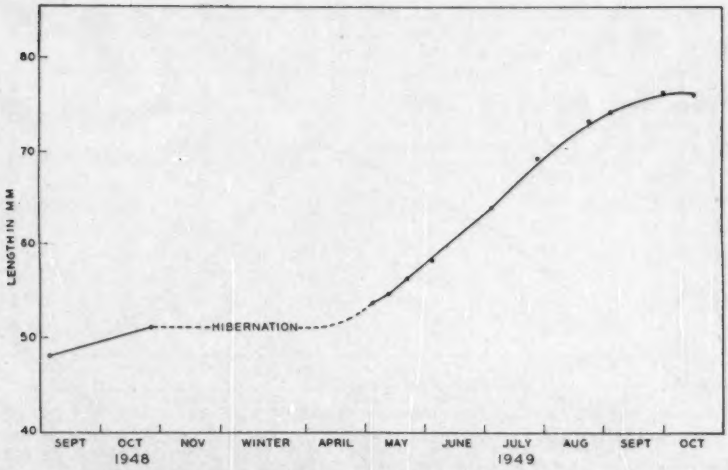


Fig. 2.—Typical growth curve as shown by actual records of a subadult green frog which probably transformed in June-July, 1948 at Loch Alpine.

Weather Station (located about ten miles from the study area) and do not show precisely the conditions that existed in the habitats of the green frogs, but they do give the general trends.

Because the frogs withdrew from the banks and were not available for capture at temperatures lower than 60 degrees F, (Martof, 1953b) the composite curve of the growth of 40-60 mm frogs was compared to the curve showing the accumulative number of hours that the temperature was above that threshold in 1949. The similarity of these curves, as shown in fig. 1, is very pronounced.

Only those frogs that grew at a rate well above the average were thought to attain a length greater than 90 mm for these reasons. First, some individuals as small as 85 mm were observed not to grow over considerable periods, strongly suggesting that they had attained maximum size. Second, the premium on large size as reflected in predation relationships may promote the survival of faster growing individuals in the population at the expense of the slower ones. Accordingly, some frogs longer than 90 mm were of the same age as, or even younger than, certain individuals in the smaller size groups. If individual records covering the entire growth cycle were available, their relationships would be evident. But in such a dynamic population as this, complete data on natural growth of individuals are limited because of the large turnover of its members. Only a small percentage of the individuals that transform on the area can be recovered when they have attained maturity. Thus a good estimate of the growth of an individual can be made on the basis of its size; however, if the age of the animal were known, a much better estimate could be computed. Since the age of a frog could not be directly ascertained in any other way than by following it from year to year, size can be but a first approximation of age.

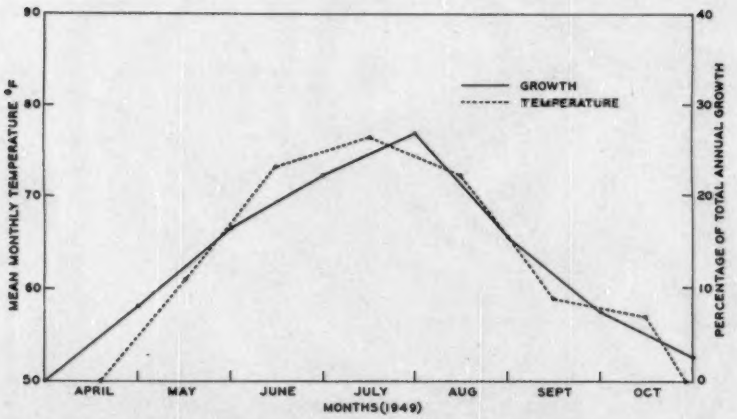


Fig. 3.—The relationship of the percentage of the total annual growth made each month by green frogs of 40-60 mm length to the average monthly temperature.

Consequently estimates of age—and length of life span—must be derived by other means. At the present, the only plausible ways of doing this are to mark or to confine individuals of known ages and to observe them periodically. Both methods have obvious limitations: the difficulty of recovering enough marked frogs to gain adequate data and the possible disturbance of natural conditions, respectively.

The amount of increase in length occurring during a season was found to be dependent upon the size of the animal. In order to gain insight into the effect of this variable, all recapture records that extended over a year (71 percent) were grouped according to size. Records of 105 frogs that met one of these requirements are summarized in table 4. As would be expected, the smallest frogs grew most rapidly, the largest ones most slowly. The rapid growth of the newly transformed frogs progressively declined, becoming greatly accentuated after sexual maturity was attained. In fact, the records of six adults did not indicate any gain in length at all; one even showed a loss of three millimeters. Raney and Lachner (1947) observed the same thing in several large toads (*Bufo terrestris*), their greatest decrease being five millimeters. It is difficult to be certain whether errors of measurement were responsible, or whether actual shrinkage occurred with old age. The growth of frogs has generally been considered to be similar to that of other poikilothermal vertebrates, especially fishes, wherein growth is asymptotic and body length indeterminate (Thompson, 1942). However, the data above suggest that size may be determinate in large frogs.

By applying the mean growth rates for the various size groups a complete growth curve was constructed (fig. 4). First the mean size at which transformation occurred, 32 mm, was plotted. Next the interpolated mean annual growth

TABLE 4.—Annual growth for transformed green frogs in the Ann Arbor area (measurements in millimeters). Estimated standard deviations of mean annual growth were obtained by use of the method outlined by Snedecor (1946).

Size group	Mean size of group	Number in sample	Mean annual growth	Est. stand. dev. of mean annual growth	Est. range of mean an. growth (88% prob.)
30- 40	36.6	13	33.6	1.08	30.3—36.9
40- 50	45.9	25	28.6	1.10	25.5—31.7
50- 60	55.1	19	23.5	.79	21.2—25.8
60- 70	64.8	16	17.8	.92	15.1—20.5
70- 80	74.6	13	8.0	.58	6.2— 9.8
80- 90	83.4	12	4.3	.49	2.8— 5.8
90-100	93.8	7	2.1	.42	0.5— 3.7

for the first year after metamorphosis, 34 mm, was added, and the estimated size at the end of the first year after transformation, 66 mm, was obtained and plotted. Then the interpolated mean annual increase in size of a frog 66 mm long was added to determine the size at the end of the second year. This value, 83 mm, was then plotted. Similarly, the estimated mean sizes for frogs at the end of the third, fourth, fifth, and sixth years after metamorphosis were obtained: 88.5, 91.7, 94.4, and 96.4 mm respectively. From the above it can be concluded that it takes an average green frog about four or five years to obtain maximum size, although it is close to its greatest length at the end of the third year after the larval stage. The short annual season of growth and the resultant long period required to attain maximum body size, no doubt, discourage commercial frog farming, especially in northern regions.

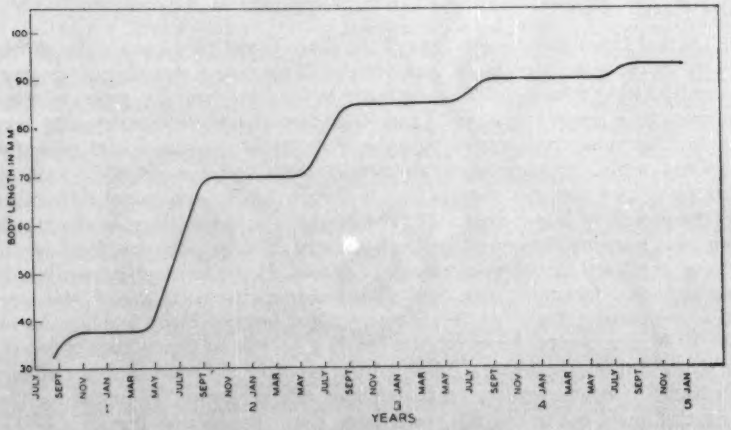


Fig. 4.—Growth curve of green frogs in the Ann Arbor area for the first 4½ years after transformation. Based on table 4.

The shape of the annual growth curve is sigmoid, and if the sequence of annual curves is superimposed on the continuous curve of growth, a compound sigmoid line is produced (fig. 4). Thompson (1942) described this phenomenon in certain fishes as "a vibration which is gradually dying out; the amplitude of the sine-curve diminishes till it disappears." He referred to this type of configuration as a "damped sine-curve." It is thought that such a curve as that for the green frog would be more or less typical for all poikilothermous vertebrates in temperate climates.

With this insight into the mean annual growth of frogs of varying sizes, one naturally thinks about age-size relationships and longevity. However, before these can be investigated some important limitations of material must be acknowledged. The establishment of age-size relationships must be viewed with great caution because of these factors: 1) The varying age and size at which transformation occurs. Age groups were very indistinct. There is much overlapping of length-frequency curves. 2) The great amount of individual variation in growth. For example, disease, injury, and developmental deformities caused retarded growth. 3) The absence of individual records covering the entire period of growth. 4) The relative paucity of data for large frogs. 5) The high premium on large size. Runts and young frogs are at a disadvantage in frog communities; they are highly vulnerable to predation by larger ones.

The life span of green frogs is not known with certainty. In fact, almost nothing appears to have been published on the subject of the duration of life of amphibians except the work of Flower (1925). His records indicate that one green frog lived ten years and two others seven years in small indoor houses at the London Zoological Gardens. They probably were at least one year old when their captivity began. Judging from the large turnover of population that was indicated on the study areas, it is doubtful if any frogs in nature attain such age. In fact, it is unlikely that any individuals get much older than five years.

Sexual Dimorphism.—Analysis of the data did not reveal any major differences in the growth of males and females. Two minor departures, however, were noted: 1) Males grew slightly faster in the 50-60 mm size group whereas females grew faster in the 60-70 and 70-80 mm groups. It is interesting that these differences corresponded to puberal spurts in growth. Males generally attained sexual maturity when about 60-65 mm and females 65-75 mm in length. There were not enough data to permit insight into sexual differences in the growth of larger frogs. 2) The stomachs of males taken in the breeding areas were invariably without food, as determined by palpation, from which it was concluded that they usually did not feed during times of intense breeding activity. This must have resulted in some retardation of growth and may have accounted entirely for the difference noted between males and females in the 70-80 mm group. However, the breeding activity of green frogs varied in intensity and during times of lull the males probably did some limited feeding. Perhaps this erratic feeding, hence decreased rate of growth, accounted for the fact that more males did not reach large size. Raney and Ingram (1941) reported a bullfrog that showed no growth in the breeding period and concluded "that this male had nearly reached his maximum length or possibly he

had not increased due to spawning activities." Because both small and large frogs showed no growth when engaged in breeding activity, I believe cessation of feeding to be the main cause of retarded growth.

Assuming that the frogs captured represented a typical sample of the local population of green frogs, the following data were compiled to test the similarity or dissimilarity of the sizes attained by males and females. Each adult frog was counted but once, regardless of the number of times it was captured, and the size at the time of last capture was used. The average body length of 344 males was 79.79 mm, with a standard deviation of the mean of 8.52 mm. Three hundred seven females had a mean size of 80.28 mm and a standard deviation of the mean of 8.86 mm. By computing the estimate of the variance of the difference of the mean and then the appropriate t-value (Kenney, 1929), a probability of .5240 was obtained. This value is obviously not significant. Therefore, the null hypothesis that the populations of males and females are the same in size is not disproved.

Of the frogs longer than 100 mm, the largest was a female, 105 mm in length. Other females were 103, 100, and 100 mm. The largest males measured 103, 101, and 100 mm.

Before considering the time of attainment of sexual maturity it is necessary to outline the methods used to recognize the sexes. In general, individuals were classified according to whether or not male secondary sexual characteristics were present. A male was distinguished by a yellow throat, an enlarged forearm and a *thumb*, and the greater diameter of the tympanum. Except for their larger size, females closely resembled subadults.

Individuals varied in the size at which sexual maturity was attained. Males generally were identified before they became 70 mm in length, and the sex of larger frogs was easily determined. However, some males were clearly recognizable when they were considerably smaller, the smallest only 58.6 mm. In contrast, the smallest female with eggs was 65.7 mm. Wright and Wright (1949) give 52 and 58 mm for the smallest male and female respectively. In all probability, these measurements are of southern specimens. Northern green frogs attain a larger mean size than do southern ones. Because of the small size of some males, one might be inclined to classify all individuals between 55 and 70 mm which did not show male secondary sexual characters as females. This would not be entirely correct because that size group was shown by recapture records to contain rapidly growing males destined to mature at a larger size. More conservatively, one might be prompted to place the 55 to 70 mm frogs in a separate category. This would be undesirable because in dealing with natural populations it is of advantage to discriminate as early as possible among individuals becoming sexually mature. Therefore, the secondary sexual characters were carefully inspected for clues permitting early classification.

Yellow pigment, which was present in the throat and surrounding regions of mature male frogs, was one useful character. It was present in great abundance during the breeding season when almost all the venter was heavily covered and even the dorsal surface of some frogs, especially the anterior part, was affected by it. Because of the darker basic color dorsally, not much of the yellow was evident; during the breeding season the males were dull-pea-green while at other times a brighter olive green coloration was observed in the

antero-dorsal region. In spite of the fact that this yellow coloration was decidedly a male characteristic it could not be used to determine the sex of maturing frogs because many 65-75 mm females had tinges of yellow pigment on the throat.

Obvious enlargement of the forearm and *thumb* were reliable criteria for sexing green frogs; however, they could not be conveniently measured.

The enlarged tympanum has long been recognized as a secondary sexual characteristic of the male in certain species of frogs (Cope, 1889). In spite of its presence in seven of the nineteen species of *Rana* in the United States and Canada (Wright and Wright, 1949), no critical attempt has been made to apply this characteristic as a means of sex recognition.

As the enlargement of the tympanum appeared somewhat earlier than other secondary sexual characteristics and was easily measured, it was used as a standard by which to sex recently matured or maturing individuals. For comparison, the already available, and perhaps most adequate, snout-to-vent measurement was chosen, and this relationship of body length to tympanum diameter is shown in figure 5. In comparing the distribution of tympanum diameter with change of body length, all records of each frog were considered at the same time. By so doing, the records of numerous individuals that later became sexually mature were observed, permitting the accurate classification of many subadult captures and consequently insight into the size at which maturity, as evidenced by a change in tympanum diameter, occurred.

Usually there was no change in the relative diameter of the tympanum

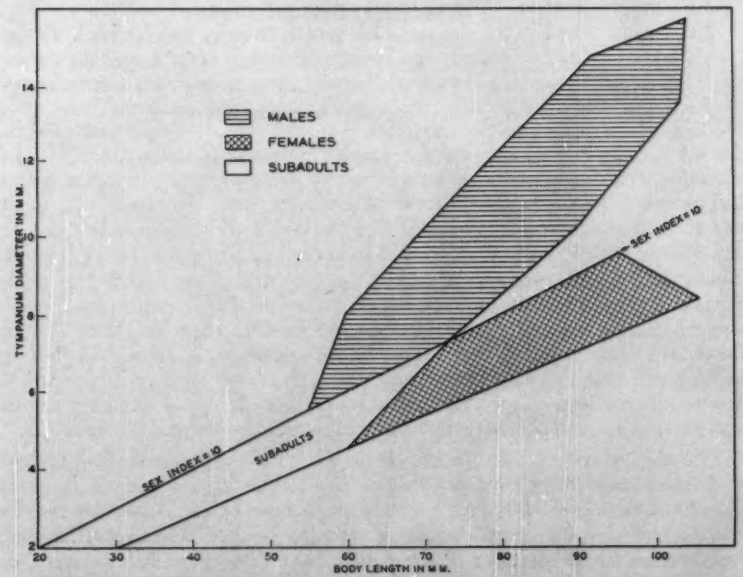


Fig. 5.—Relationship of tympanum diameter to body length as shown by 2,018 records. Lower limits for each sex are based on individuals identified at later captures.

throughout the life of a female green frog. After sexual maturity females maintained approximately the same position in the distribution as was previously occupied. As a result the subadults and the sexually mature females formed a continuous group (fig. 5).

A very applicable *rule of thumb* for field recognition of sex was produced as follows. The ratio of the body length to the tmypanum diameter was obtained for all adults and most subadults. Very conveniently this ratio (which will be referred to as the *sex index* generally was below ten for sexually mature males and above ten for females and sub-adults. This critical value, sex index of ten, is represented in figure 5 as the upper limit of the subadult-female group.

$$\text{Sex index} = \frac{\text{body length}}{\text{tympanum diameter}}$$

The mean sex index of 633 adult males was calculated to be 8.3. Of these, the 250 taken in the breeding ponds had an average sex index of 7.7. The range for all males was from 6.7 to 10.2. The 682 adult females captured had a mean sex index of 11.3; this was the same mean index as that ascertained for 703 subadults. The range for females and subadults was 9.7 to 14.5.

It is obvious from the above data that a region of overlap occurs. Accordingly, the sex index is not a perfect solution of this problem, but it is valuable. It is easily applied and even in the region of the overlap there was not as much difficulty as might, at first, be expected. Most frogs in this group were readily classified and with a high degree of accuracy. In general, those above 70 mm were proven by later captures to be females and smaller ones males. Males above 70 mm usually had a considerably larger tympanum, hence a smaller sex index. The small frogs with sex indices in the region of the overlap were for the most part males that were developing secondary sex characteristics.

Differential enlargement of the tympanum of the male did not occur prior to attaining a body length of more than 50 mm. This limit was selected because a frog taken Aug. 9, 1949 in the breeding area at Hogback was only 58.6 mm in length but already had a sex index of 7.5. Most males, however, became sexually mature, as judged by tympanum proportions, when about 60-65 mm long. The largest size at which a male was found to mature was 72 mm.

Females, on the other hand, could not be identified at such small size; in fact, it was only after differentiation of the males had begun that some females were recognized. As mentioned, the smallest female with eggs was 65.7 mm; which suggests that they very probably did attain sexual maturity at a size similar to the males but since more time is required for development of their gametes, they were usually about 75 mm in length or larger. In fig. 5 the lower size limit for females was established because no individuals in this area developed into males and many were proved by recapture to be females.

For analysis of individual records it seemed generally true that green frogs did not reach sexual maturity until the season following metamorphosis. Late in the season in which sexual maturity was attained these males moved to the breeding area and actively took part in calling, from which it is presumed,

until further evidence is available, that they were capable of reproduction. Females of comparable age did not go to the breeding areas until the season following attainment of maturity. This early participation in reproductive activities may cause retardation in the growth of males.

SUMMARY

In 1948 and 1949, 3402 captures of 2264 green frogs were made on two study areas near Ann Arbor, Michigan. All frogs were marked, examined, and released at the place of capture. Records were carefully made of the snout-to-vent measurement and of the tympanum diameter of each captured frog.

Contrary to published accounts, the larval life of green frogs was found to be as short as 70 to 85 days or as long as 335 to 360 days depending on when the eggs were laid. Those deposited before about June 25 developed into metamorphosed frogs later the same year; those laid after about July 10 did not develop beyond the tadpole stage until the following year. Eggs laid between June 25 and July 10 may or may not develop into frogs in the same season.

The season of growth, as indicated by an increase in the snout-to-vent measurements of transformed frogs, is primarily from mid-May to mid-September, with most of it in June and July. Analysis showed it to be closely correlated with the mean monthly temperature and the number of hours that the temperature was favorable for feeding, i.e., above 60°F. The shape of the annual growth curve is sigmoid.

At the time of transformation, the length of 286 green frogs ranged from 28.4 to 36.3, with the mean at 32.6 mm. During the first year after metamorphosis the average green frog grows about 34 mm and 17.0, 5.5, 3.2 mm during the second, third, and fourth years respectively. Thus it takes on the average about four or five years for an individual to grow from the egg stage to very near maximum size. If the annual growth curve is superimposed on the continuous curve of growth as it occurs throughout the life of an individual, a compound sigmoid curve is produced.

Sexual maturity is attained about a year after transformation, but generally these recently matured frogs do not become sexually active until the following year. No marked sexual dimorphism in maximum size was indicated for the largest female measured 105 mm, the largest male 103 mm.

The sex of an adult frog can generally be ascertained from the ratio of body length to tympanum diameter, the sex index. If the sex index is less than ten, the individual is a male; if the index is ten or more and the frog larger than about 70 mm in body length, it is a female; otherwise, the animal may be classified as a subadult.

REFERENCES

ADOLPH, E. F. 1931—The size of the body and the size of the environment in the growth of tadpoles. Biol. Bull. 61:350-375.

ANGEL, F. 1946—Faune de France. Vol. 45, Reptiles et Amphibiens. Paris, Paul Lechevalier.

BURGESS, R. C. JR. 1950—Development of Spade-foot toad larvae under laboratory conditions. Copeia 1950(1):49-51.

COPE, E. D. 1889—The Batrachia of North America. U. S. Nat. Mus. Bull. 34.

DAVENPORT, C. B. 1899—Experimental Morphology Part 2. Effect of Chemical and Physical agents upon growth. New York, MacMillan.

DEMPSTER, W. T. 1930—The growth of larvae of *Ambystoma maculatum* under natural conditions. Biol. Bull. 58(2):182-192.

FLOWER, S. S. 1925—Contributions to our knowledge of the duration of life in vertebrate animals, II Batrachians. Proc. Zool. Soc. London 269-289.

FORCE, E. R. 1933—The age of the attainment of sexual maturity of the leopard frog *Rana pipiens* (Schreber) in Northern Michigan. Copeia 1933(3):128-131.

HAMILTON, W. J. JR. 1934—The rate of growth of the toad (*Bufo americanus americanus* Holbrook) under natural conditions. Ibid. 1934(2):88-90.

HOLZAPFEL, R. 1937—The cyclic character of hibernation in frogs. Quart. Rev. Biol. 12:65-84.

KENNEY, J. F. 1939—Mathematics of statistics. Part II. New York, P. Van Nostrand.

KLIMSTRA, W. D. 1949—Early bullfrog transformation. Copeia 1949:231.

LYNN, W. G. AND A. EDELMAN 1936—Crowding and metamorphosis in the tadpoles. Ecology 17:104-109.

MARTOF, B. 1953a—Territoriality in the green frog, *Rana clamitans*. Ibid. 34:165-174.

——— 1953b—Home range and movements of the green frog, *Rana clamitans*. Ibid. 34:529-543.

——— In Press—Factors influencing size and composition of populations of *Rana clamitans*. Amer. Midl. Nat.

PATCH, E. M. 1927—Biometric studies upon development and growth in *Ambystoma punctatum* and *tigrinum*. Proc. Soc. Exp. and Med. 25:218-219.

RANEY, E. C. AND W. M. INGRAM 1941—Growth of tagged frogs (*Rana catesbeiana* Shaw and *Rana clamitans* Daudin) under natural conditions. Amer. Midl. Nat. 26(1):201-206.

——— AND E. A. LACHNER 1947—Studies on the growth of tagged toads (*Bufo terrestris americanus* Holbrook). Copeia, 1947(2):113-116.

SCHAPER, A. 1902—Beiträge zur Analyse des thierischen Wachstums. Eine kritische und experimentelle Studie. 1 Thiel: Quellen, Modus und Lokalisation des Wachstums. Roux Archiv 14(3):307-400.

SNEDECOR, G. W. 1946—Statistical methods applied to experiments in agriculture and biology. Ames, Iowa, Iowa State College Press.

SWINGLE, W. W. 1919—Iodine and the thyroid. III. The specific action of iodine in accelerating amphibian metamorphosis. J. Gen. Physiol. 1:593-606.

——— 1919—Iodine and the thyroid. IV. Quantative experiments on iodine feeding and metamorphosis. Ibid. 2:161-171.

——— 1922—Experiments on the metamorphosis of neotenous amphibians. J. Exp. Zool. 36:397-421.

THOMPSON, D. A. W. 1942—On growth and form. Cambridge, Cambridge Univ. Press.

TING, H. 1951—Duration of the tadpole stage of the green frog, *Rana clamitans*, Copeia 1951:82.

WALKER, C. F. 1946—The amphibians of Ohio. Part I. The frogs and toads. Columbus, Ohio. Archaeol. and Hist. Soc.

WILDER, I. W. 1924—The relation of growth to metamorphosis in *Eurycea bislineata* (Green). J. Exp. Zool. 40:1-112.

WRIGHT, A. H. 1914—North American Anura; life histories of the Anura of Ithaca, New York. Carn. Inst. Wash. Publ. 197.

——— 1932—Life-histories of the frogs of Okefinokee Swamp, Georgia. North American Salientia (Anura) No. 2. New York, Macmillan.

——— AND A. A. WRIGHT 1949—Handbook of frogs and toads. Ithaca, Comstock.

Age and Growth of Two Important Bait Species in a Cold-Water Stream in Southern Illinois

Gerald E. Gunning and William M. Lewis
Southern Illinois University, Carbondale

The majority of bait species used by anglers in southern Illinois are those species that are obtained from the wilds. The stoneroller (*Campostoma anomalum*), golden shiner (*Notemigonus crysoleucas*), bluntnose minnow (*Pimephales notatus*), and creek chub (*Semotilus atromaculatus*) respectively, are the most important species used. This paper is concerned with the age and growth of two of these species, namely the creek chub and stoneroller (fig. 1).

The area of study was a small, spring-fed stream six miles south of Anna, Illinois. The stream is known locally as Roaring Springs Creek, however it is more properly designated as the headwaters of Millcreek, a tributary of the Cache River. The majority of the water in the stream comes from a large spring at the headwaters. The stream flows at an average rate of 450 gallons per minute. The area surrounding the stream is underlaid by Mississippian limestone which varies in thickness from 20 to 550 feet. The approximate length of the stream is two miles with an average width of eight feet. The stream is in the form of pools and riffles with the pools ranging in depth from two to five feet. Water temperature along the entire stream during July

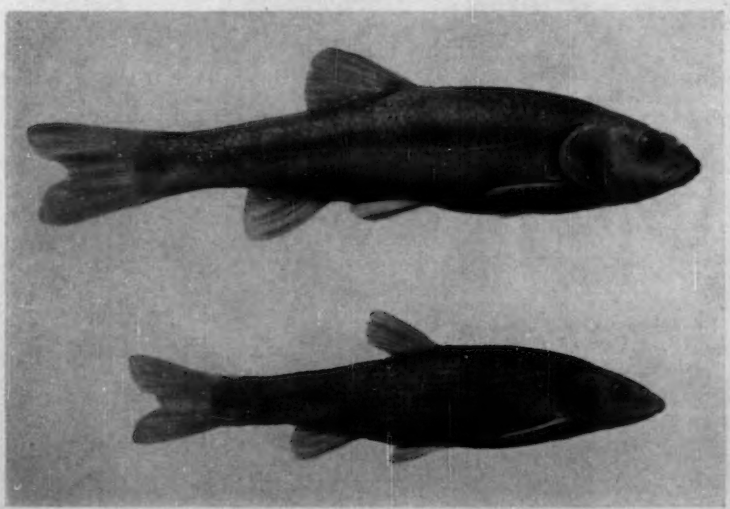


Fig. 1.—The creek chub (upper) and the stoneroller (lower) are two of the principal bait minnows used in Southern Illinois.

ranged from 54 to 60° F. Due to its inaccessibility, Roaring Springs Creek has not been seined by commercial bait dealers.

METHODS

Seven collecting stations were set up along the two miles of stream commencing at the headwaters and terminating where Roaring Springs Creek empties into Millcreek. The fish population was sampled with an electrofishing device and one-quarter inch bar measure, knot seine. The electrofishing device consisted of a 230 volt, alternating current, portable generator equipped with hand electrodes. A sample at a particular station consisted of the majority of fish contained in a pool and its surrounding riffles. Age determinations were made independently both by the scale method and by the length-frequency distribution method. Body length-scale radius relationship was calculated and the values determined were utilized in the calculation of prior growth. The relationship for stonerollers was described by a straight line with an intercept of 13 millimeters on the length axis and with a slope of

TABLE 1.—Growth rates of fish taken from Roaring Springs Creek in August, 1954.[1]

Age group	Number of fish	Average standard length at capture (millimeters)	Calculated standard length (millimeters) at end of year 1	2	3	4
			Stonerollers			
0	7	40	....	....	....	....
I	11	59	40	....	....	....
II	59	74	42	63	....	....
III	13	88	43	67	83	....
Mean standard length (millimeters)			42	65	83	
Total length (inches)[2]			2.0	3.1	3.9	
Annual length increment (millimeters)			42	23	16	
			Chubs			
0	10	55	....	....	....	....
I	81	72	48	....	....	....
II	54	94	50	75	....	....
III	8	121	51	77	108	....
IV	1	143	51	83	112	133
Mean standard length (millimeters)			50	78	110	133
Total length (inches)[3]			2.3	3.7	5.2	6.3
Annual length increment (millimeters)			50	28	30	21

[1] Sexes combined.

[2] Length conversion based on 88 specimens ranging from 38 to 143 millimeters of standard length: total length (inches) equals 0.047 standard length (millimeters); standard length (millimeters) equals 21.37 total length (inches).

[3] Length conversion based on 102 specimens ranging from 38 to 143 millimeters of standard length: total length (inches) equals 0.047 standard length (millimeters); standard length (millimeters) equals 21.39 total length (inches).

6.74. The relationship for creek chubs was described by a straight line with an intercept of 12 millimeters on the length axis and with a slope of 3.36. Measurements of the projected scale images were taken along the anterior radius.

RESULTS

If one takes into consideration that the length frequency distribution is an age estimate method applicable to the younger age groups and those that are well represented, the stoneroller ages determined by this method closely approximate those obtained by the scale method. Ages O, I, II, and III were represented (Table 1). Age group II was the most abundant, making up 65 percent of the stoneroller sample. A length-frequency distribution analysis of a population of stonerollers in another stream in the vicinity showed representation of ages O, I, and II (Lewis and Elder, 1953). Ohio studies showed representation of classes I, II, and III (Carlander, 1950). The stoneroller probably has a life span of three years.

The stonerollers in Roaring Springs Creek reached a usable length (three inches total length) at the end of their second summer of growth (Table 1). The growth in Roaring Springs Creek was significantly slower than the growth reported for Clear Creek (Lewis and Elder, 1923) and for the Ohio study (Carlander, 1950).

The length-frequency distribution of creek chubs failed to show discrete modes. All comments on age and growth are therefore based on the scale method. Ages O, I, II, III, and IV were represented (Table 1). Ages I and II were more abundant. Again in comparison to other studies this age distribution appears normal. The fish probably is a short-lived one. The creek chubs reached a usable bait length (three inches total length) during their second summer of growth. The rate of growth of the Roaring Springs Creek sample was comparable to the values reported for Ohio but significantly below those reported from the other southern Illinois study (Lewis and Elder, 1953), and below values reported from Quebec (Carlander, 1950).

Acknowledgments.—Thanks are due Messrs. Darrell Louder, Charles Peters, and Jerry Hord for assistance in carrying out the necessary field work.

This was a cooperative study between the Zoology Department of Southern Illinois University and the Division of Fisheries, Illinois Department of Conservation. Mr. Sam Parr cooperated on behalf of the Division of Fisheries.

REFERENCES

CARLANDER, KENNETH D. 1950—Handbook of freshwater fishery biology. Wm. C. Brown Company, Dubuque, Iowa.

LEWIS, WILLIAM M., AND DAVID ELDER 1953—The fish population of the headwaters of a spotted bass stream in southern Illinois. Trans. Amer. Fish. Soc. 82(1952): 193-202.

Notes on the ecology of Zonitoides arboreus (Say), Opeas pumilum (Pfeiffer), and Lamellaxis gracilis (Hutton) in greenhouses.

Edward J. Karlin
Cornell University, Ithaca, N. Y.

During the course of this study, eight greenhouse ranges,[1] devoted exclusively to the commercial production of roses, were investigated for snail populations. The ranges were located in five counties of New York State as follows: Suffolk, four; Nassau, one; Chemung, one; Niagara, one; Monroe, one. They varied in size from a range consisting of four greenhouses to one composed of 29 greenhouses with over 100 benches of roses in production. Specimens of at least one of three species of mollusks, *Zonitoides arboreus* (Say), *Opeas pumilum* (Pfeiffer), or *Lamellaxis gracilis* (Hutton), were found in all of the ranges. A single, dead, specimen of *Cionella lubrica* (Müller) was the only other shelled mollusk found in any of the houses.

All three snail species have been recorded as part of the greenhouse fauna of Europe (Meeuse and Hubert, 1949) but no discussion of their ecology appeared in the very extensive paper. Indeed, all of the literature on these three species contains very few ecological references.

The ecological factors investigated in this study are discussed under the following headings: Soil, Temperature, Moisture, Food, Population Dynamics, and Distribution.

Soil.—Commercially grown roses are planted as seedling root stocks in beds ranging from 50 to 300 feet in length and two to six feet in width with an approximate soil depth of 18 inches. A bed may be in production as long as seven years without replanting. Frequently, different beds within one greenhouse are planted with rosebushes of different ages. When planting takes place, the soil is steam sterilized. This process is intended to destroy nematodes and other plant pests. Undoubtedly, when properly carried out, the snails or snail eggs present are also killed. In most cases, a sterilized mulch is then spread over the soil surface or the beds may be left with a bare soil surface. The snails reported here were found in beds with, and those without, mulch. When mulch was present it consisted of 1) manure, 2) manure and straw, 3) corn cobs, 4) corn cobs and manure, 5) corn cobs and buckwheat hulls, or 6) buckwheat hulls alone. The primary purpose of this mulch was to hold moisture, and corn cobs which are quite effective for that purpose were found in most of the beds, either alone or in some combination. All eight ranges studied made some use of cobs while manure was used extensively only in one range and buckwheat hulls in limited quantities in one other.

[1] A group of greenhouses, usually connected, under one management is considered to be a range.

The pH of the soil invariably was somewhat less than neutral. Sixty soil samples taken at the Chemung County range in June of 1954 and electrically tested at the Cornell University Soils Laboratory gave a pH range of 5.5 to 6.2 with a mean of 5.9. These figures were of vertical samples including soil from several inches in depth. They were in close agreement with those for six samples taken by a random method in the Nassau County range and tested by a colorimetric method, resulting in a range of 5.6 to 5.9. The latter samples were obtained at the soil surface where snails are normally found and included some mulch as well as soil. All three species, *Z. arboreus*, *O. pumilum*, and *L. gracilis*, occurred at the Nassau County sampling sites while only *Z. arboreus* occurred in the beds sampled at the Chemung County range. Ingram (1945) found *Z. arboreus* in hemlock forests, typically acid areas, but in most molluscan studies, field workers have reported positive correlations between high snail populations and high pH readings. Therefore, the presence of thriving snail colonies on decidedly acid soils as herein reported appears to be quite an anomaly. However, there is a reasonable explanation. It is a common horticultural practice, particularly in the sandy soils of Nassau and Suffolk counties, to add gypsum or some similar substance to the soil of rose houses. This practice increases the calcium content without raising the pH as would the addition of lime. The Cornell University Soils Laboratory reported that the 60 soil samples had a water soluble calcium range of 115 to 135 parts per million with a mean of 126.45 parts. The potassium present averaged 25.58 parts per million and the phosphorus, 9.36 parts per million. Although the minimum requirements of these minerals have not been established for snails, the large number of individuals present, even in the beds with the lower pH readings, gives a strong indication that the amounts of minerals found are well within the limits of tolerance for the snails. Evidently, pH alone cannot be considered as a critical factor.

Temperature.—The literature references indicate that *O. pumilum* and *L. gracilis* are tropical snails. *Z. arboreus* ranges from the tropics to the northern part of the north temperate zone. Thus, the first two species would be expected to thrive best in high temperatures while the latter species should display greater resistance to low temperatures. Actually, all three appeared to have no difficulty withstanding the temperature range within the greenhouses where summer temperatures occasionally rose as high as 115°F and artificial heating prevented winter temperatures from dropping below 56°. During the summer, vents were opened to aid in maintaining an ideal range between 60° and 80°F.

Since all three species of snails occurred on the soil beds, they received some shading from the growing plants. Consequently, the summer temperatures of their immediate habitat were somewhat more moderate than elsewhere in the houses.

Moisture.—Moisture undoubtedly was an important factor in determining which species of snails were present. It may be stated emphatically that all the greenhouses investigated were "wet." Pools of water often occurred in the aisles between the rose benches. Beds were thoroughly watered two to three times a week and the plants were often syringed in hot weather. This procedure increased the humidity and also impeded the development of colonies

of spider mites. Condensation on the foliage was commonplace and the bed soil invariably felt damp to the touch. Humidity measurements were taken five days after the beds had been watered in one of the Nassau County greenhouses. These measurements were made at noon at heights of one and six feet above the bed soil. At 77°F relative humidities of 66% and 73% were obtained with a hand-aspirated psychrometer. Although the humidity varied daily, these figures may be taken as representative of the usual high range. The readings would have been higher if the measurements had been made more closely following the time of watering.

Food.—The literature describes the Zonitidae and the Achatinidae[2] as herbivores. In this study, no snail was found more than one inch above the soil surface. Therefore, it may be assumed that the snails fed only on plant matter in the mulch and did no damage to the rose blossoms or foliage. This is in contrast to the situation in commercial orchid-growing greenhouses where *Z. arboreus* feeds on the flower petals and is considered an important economic pest by the growers.

Population Dynamics.—Four of the ranges studied contained colonies of two or more species of snails. In those ranges, the distribution varied qualitatively and quantitatively from bed to bed and greenhouse to greenhouse, but in no clearly discernible manner. Numbers appeared to vary with the amount of mulching, the heavier the better. The beds of older plants also contained larger snail colonies.

Relative population counts for the three snail species were made in daylight by counting all specimens, dead or alive, in three, one-foot-square plots. These plots were chosen at random from a bed 140 feet long and three feet wide. The bed was selected since it contained a large population of *Z. arboreus* as determined by the number of easily visible dead shells in the mulch. The same procedure was followed with another bed containing large numbers of *Opeas* and *Lamellaxis*. In the first bed, there was an average ratio of 88 *Zonitoides* to 43 *Opeas* to zero *Lamellaxis* per square foot. The second series of samples gave an average ratio of three *Zonitoides* to 96 *Opeas* to 16 *Lamellaxis* to 29 Achatinidae. This last category was necessitated by the difficulties of separating partially broken, empty shells of *Opeas* and *Lamellaxis*. A few non-randomly selected plots which contained approximately equal numbers of all species were also found in each of these two beds.

Within the houses of the Nassau Coutny range, beds were found with only *Opeas*, with only *Lamellaxis*, with only *Zonitoides*, and with all three mixed in varying proportions. Observations on 22 beds indicated that the achatinids occurred alone on four beds which were in heavy corn cob mulch and occurred in greater numbers than *Z. arboreus* on five other beds which were heavily mulched with cobs. In contrast, beds which contained little mulch or a manure and straw mulch were supporting populations composed mainly of *Zonitoides*. Thus, indications are clear that the achatinids favor or are favored by a cob mulch; *Z. arboreus*, by the other types of mulch. This difference may lie in a greater ability of the latter species to withstand desiccation. Microhumidity

[2] *Opeas* and *Lamellaxis* are two genera of the family Achatinidae.

measurements made by the capillary tube method of Nielson and Thorndrup (1939) gave readings of greater than 90% relative humidity in the interstices of corn cobs in the mulch while readings of less than 80% were recorded from the other organic litter in the same beds. These readings were made five days after the beds had last been watered. Few shells of any species were found on beds which contained no mulch but it is uncertain whether this difference was due to variations in moisture, temperature, food, or a combination of all of these factors. Since population counts included empty shells as well as living snails, the total population of live individuals at any one time might be expected to have been appreciably less than the figures given. Nevertheless, night observations of *Z. arboreus* at the Chemung County range indicated live populations with 23, 39, and 46 individuals in three randomly selected one-foot-square plots. The counts were made just after the onset of darkness, before the snails had left the beds in any numbers but after they had become active and were easily located. Thus, the totals may be assumed to represent an accurate appraisal of the living population. The counts were approximately equal to those for empty shells in the same plots. There were many young individuals in the live population, however, a factor which would vary throughout the year and which probably contributed to the high ratio of live to dead snails.

Distribution.—These snails were found to be almost universally distributed within the greenhouses investigated. During the day, living individuals were very difficult to find since they sought the deepest interstices of cobs, mulch, and soil. However, after nightfall, living snails were found in the aisles, on the heating pipes, and on the sides of the benches as well as in the beds. At least one specimen of *Z. arboreus* was observed to crawl from a bed to the adjacent one in less than 30 minutes. However, the snails moved in such a manner that they most often returned to the beds from which they had departed. Activity within the beds was widespread. Given time, distribution could have occurred from bench to bench and greenhouse to greenhouse since the latter are usually connected within a range. Because of this nocturnal movement, a potential source of infestation always remains in established ranges where all the benches are never emptied or sterilized at once. In addition, eggs and snails occur outside of the soil areas, on the pipes and in the aisles. These foci would not be reached by sterilization of the soil, even if it were a completely effective job which it often is not.

Z. arboreus, a common member of the indigenous fauna of New York State, may conceivably reach newly erected or non-colonized greenhouses by its own efforts or in the "sterilized" soil which usually has a local origin. The snails may also be introduced on root stocks brought in from other ranges, even from as great a distance as California and Arizona where root stocks are commonly grown out-of-doors. Field investigations should be made particularly for *Opeas* and *Lamellaxis* in those regions since the climate appears suitable for such tropical species.

SUMMARY

Zonitoides arboreus (Say), *Opeas pumilum* (Pfeiffer), and *Lamellaxis gracilis* (Hutton) were found commonly in eight greenhouse ranges in New

York State. Roses were the only crop grown in those greenhouses.

The roses were grown on steam sterilized soil covered by a mulch of corn cobs, manure, straw, buckwheat hulls, or some combination of those constituents.

The pH of the soil in the beds ranged from 5.5 to 6.2. Nevertheless, because of fertilizing procedures, the water-soluble calcium content of the soil was high with a mean of 126.45 parts per million at one range.

There was an attempt to maintain an ideal temperature range of 60° to 80° F. This range was found to be suitable for the development of the snail colonies as were the very wet conditions which prevailed. Five days after the beds had been watered, humidity measurements greater than 90% relative humidity were recorded in the mulch. The relative humidity of the greenhouse air was approximately 70% on the same day.

All of the species of snails are herbivorous. Nevertheless, they were of no economic significance but apparently fed only on plant matter in the mulch.

All three snail species varied in total and proportionate numbers from bed to bed and greenhouse to greenhouse. The maximum population of living snails plus empty shells per square foot of bed soil was approximately 90 *Zonitoides*, 90 *Opeas*, and 16 *Lamellaxis*. Observations of living *Zonitoides* in one bed gave a maximum of 46 individuals per square foot, a number approximately equal to the dead snails in the same plot. Many of the living snails were immature individuals and the count might have been appreciably smaller had it been made a few days earlier.

Beds with corn cobs as a component of the mulch appeared best for the development of *Opeas pumilum* and *Lamellaxis gracilis*. *Z. arboreus* was consistently less common in beds with a heavy mulch of cobs. However, all three species were more abundant in beds with mulch than in beds without.

New populations of snails are likely to occur in rose houses because of the cultural practices followed.

The snails were found to move over considerable distances with almost all movement restricted to the hours of darkness.

Acknowledgments.—Sincere thanks are due to Dr. Henry van der Schalie of the Museum of Zoology, University of Michigan, and Mr. M. K. Jacobson of the New York Shell Club who identified all of the molluscan species. Appreciation is also expressed to Dr. C. O. Berg of the Dept. of Entomology and Limnology, Cornell University, who kindly read and criticized this manuscript.

REFERENCES

INGRAM, W. I. 1945—Land Mollusca of the Edmund Niles Huyck Preserve, Rensselaerville, N. Y. Nautilus 59:87-93.

MEEUSE, A. D. J. AND B. HUBERT 1949—The mollusc fauna of glasshouses in the Netherlands. Basteria 13:1-30.

NIELSON, E. T. AND H. M. THORNDRUP 1939.—Ein Hygrometer für microklimatische Untersuchungen. Bioklomat. Beibb. 6:180-184.

Studies on the Filth Flies at the University of Michigan Biological Station, Douglas Lake, Michigan —Summer 1954*

Roger W. Williams[1, 2]
Columbia University, New York, N. Y.

The relationship of flies, particularly those which are attracted to decaying organic matter for feeding and/or breeding purposes, to pathogenic organisms of man has long been established. During the 1940's some such flies were shown by various investigators to be naturally infected with the virus of poliomyelitis. This virus-fly relationship, and later the consideration given to the possibility of the intentional introduction of certain fly-borne diseases, led to the investigation of the nature of the total fly population of various communities and urban fly control was greatly stimuated. As an outgrowth of such investigations new biological facts regarding some of these flies has come to light (Williams, 1954).

The present study was undertaken to determine what species of flies at the University of Michigan Biological Station, in Cheboygan County, Michigan, are commonly attracted to decomposing fish; the percent of the total population represented by each species; species population peaks in time; and species preference as to local habitat, whether near the kitchen close to the human food supply or whether on the beach where an occasional dead fish washed onto the shore attracted many flies and where these flies were at times most disconcerting to those people living in beach cabins.

Procedure

Efficient fly traps, which were built over 30 years ago of an unconventional design for the purpose of fly control, were utilized. Fish was chosen as the bait since it is generally accepted that a greater number of fly species are attracted to it than to other baits. One baited trap was placed near the kitchen door (a community kitchen and dining hall served all those attending the camp) every other day and on alternate days one was placed on the beach. A distance of approximately 600 feet and a number of intervening buildings separated these two collecting localities. The flies from each trap were identified at the end of each trapping day. Since this investigation was carried on simultaneously with others it was not always possible to leave traps the same length of time in both localities over any given 48 hour period. Usually the trap at the

---

* Contribution from the University of Michigan Biological Station.

[1] School of Public Health and Administrative Medicine, Columbia University.

[2] I wish to express my gratitude to Dr. Curtis Sabrosky of the U. S. National Museum for the identification and verification of certain sample fly specimens and to Dr. Willis W. Wirth of the same institution for the identification of *Curtonotum helvum* (Loew).

kitchen operated for a longer period per trapping day. To compensate for this two more daily collections were made on the beach with the result that between June 21 and August 10, 1954, 18 collections were made near the kitchen door and 20 were made on the beach. This procedure made for roughly an equal amount of trapping time at each locality.

RESULTS

An analysis of the fly population, represented by 17,146 flies, attracted to fish bait during the summer session at the University of Michigan Biological Station is given in table 1. The species will be discussed in the order of their overall frequency.

Phormia regina (Meigen) represented 52 percent of the total fly catch with 8,845 specimens taken. Fifty-three percent of this species were taken in the beach trap and the peak of population was reached during the 10 day period between July 11 and 20.

Lucilia illustris (Meigen), taken 2,995 times, made up 17 percent of all the flies trapped. The population peak was reached between July 21 and 30, 10 days later than for *P. regina*. The beach trap captured 56 percent of this species.

Ophyra leucostoma (Wiedman) which was taken 1,991 times, represented 12 percent of the overall catch. Sixty percent were taken at the kitchen and the peak of the population was reached between July 21 and 30 (consideration must be given to the number of collecting days in each 10 day period—see table 1).

Sarcophaga spp. (see table 1 for some of the species thought to be represented), which composed 6 percent of the total catch with 1,086 trapped, were much more common on the beach where 84 percent were captured. The greatest number were taken during the 6 collecting days between June 21 and 30.

Hydrotaea houghi Malloch and *H. occulata* (Meigen) were captured 1,040 times and made up 6 percent of the total fly population. Fifty-three percent were taken in the beach trap. *H. houghi* was far more prevalent than *H. occulata*. These two species were somewhat more abundant during the 10 day period of July 1 to 10 than during subsequent periods.

Hylemya cilicrura (Rondani) and *H.* sp. were more common on the beach where 69 percent of the 222 individuals taken were captured. The population peak of these species, of which *H. cilicrura* was the dominant one, was reached during the 10 day period of July 11 to 20.

Muscina assimilis (Fallen), of which 203 specimens were taken, was captured 61 percent of the time on the beach. The peak population was reached during the first 10 days of August.

Fannia spp. (see table 1 for the species) were somewhat more numerous near the kitchen where 57 percent were captured. Sixty percent were taken during the first 10 days of August.

TABLE 1.—The more common filth flies attracted to fish bait, University of Michigan Biological Station, Douglas Lake, Michigan. Summer 1954

Species**	Total No. Trapped	Number Trapped at: Kitchen 18 coll. days	Number Trapped at: Beach 20 coll. days	Number Trapped by 10-day Periods: June 21-30 6 coll. days	July 1-10 8 coll. days	July 11-20 8 coll. days	July 21-30 7 coll. days	Aug. 1-10 9 coll. days
Phormia regina	8,845(52)†	4,141(47)	4,704(53)	854(9)	1,029(12)	2,966(34)*	2,180(25)	1,816(21)
Lucilia illustris	2,995(17)	1,323(44)	1,672(56)	334(11)	543(18)	729(26)	932(31)*	394(13)
Ophyra leucostoma	1,991(12)	1,213(60)	778(40)	37(2)	113(6)	451(23)	665(33)*	725(37)
Sarcophaga aldrichi‡ bullata, coloradensis, rapax, sinnata, stimulans, spp.	1,086(6)	172(16)	914(84)	295(27)*	138(13)	215(20)	162(15)	276(25)
Hydrotaea hughi, occulata	1,040(6)	485(47)	555(53)	152(15)	271(26)*	228(22)	227(22)	162(15)
Hylemya cilicrura, sp.	222(1)	68(31)	154(69)	19(9)	48(21)	90(41)*	42(19)	23(10)
Muscina assimilis	203(1)	80(39)	123(61)	15(7)	9(9)	53(26)	49(24)	67(33)*
Fannia americana, canicularis, manicata, scalaris, sp.	200(1)	115(57)	85(43)	0(0)	1(0)	35(17)	45(23)	119(60)*
Phaenicia sericata	159(1)	95(60)	64(40)	13(8)	46(29)*	29(18)	32(26)	39(18)
Bufolucilia silvarum	118(1)	58(49)	60(51)	12(10)	20(17)	37(31)	38(22)*	11(9)
Muscina stabulans	98(1)	76(78)	22(22)	4(4)	15(15)	33(34)*	23(23)	23(23)
Musca domestica	44(0)	27(61)	17(39)	0(0)	0(0)	0(0)	12(27)	32(73)*
Calliphora vicina	40(0)	27(67)	13(33)	9(23)	6(15)	3(8)	9(23)	13(33)*

** For other species trapped, see text

† Percent of total number trapped to nearest whole number shown in parentheses

* Population peak for the species indicated

‡ Species of *Sarcophaga* found identified in the collection of the Biological Station (identified by M. H.)

Phaenicia sericata (Meigen) taken only 159 times was trapped 60 percent of the time at the kitchen. The population peak was attained between July 1 and 10.

Bufolucilia silvarum (Meigen) was taken 118 times, 51 percent being trapped on the beach. The population reached its peak between July 21 and 30.

Muscina stabulans (Fallen), of which 78 percent of 98 specimens were taken near the kitchen, reached its greatest density of population between July 11 and 20.

Musca domestica L. was taken 61 percent of the time near the kitchen, however only 44 were captured. Thirty-two of these were taken in the August trapping period.

Calliphora vicina Robineau-Desvoidy, taken 40 times, was captured 67 percent of the time near the kitchen. This species seemed to have just passed a peak of population density in the latter part of June, decreased in number during the warmer part of the summer and then increased again during the first part of August.

Other species trapped were 18 *Limnophora arcuata* Stein taken 13 times in the beach trap, 15 *Calliphora vomitoria* (L.) captured 8 times in the beach trap, 13 *Paregle cinerella* (Fallen) captured 9 times in the beach trap, 12 *Cynomyopsis cadavarina* (Robineau-Desvoidy) trapped 6 times at the beach, 10 *Fucellia maritima* (Hall) taken 6 times at the beach, 5 *Calliphora terraenovae* Macquart captured 3 times at the beach, 4 *Archytas spicifera* Walker, all of which were taken in the beach trap, 4 *Cyanus elongata* (Hough) all from the kitchen trap, 3 *Callitroga macellaria* (Fabricius) taken on the beach, 3 *Curtonatum helvum* (Loew) from the kitchen trap, 2 *Belvosia canadensis* Curran in the beach trap, 2 *Calliphora coloradensis* Hough in the kitchen trap, 2 *Lispe tentaculata* (Degeer)—one from each trapping area, 2 *Mydea* sp. in the beach trap, 2 *Peleteria anaxias* (Walker) in the kitchen trap; a single specimen of each of the following was captured: *Alloeostylus diaphanus* (Wiedmann), *Coenosia tigrina* (Fabricius), *Helina troene* (Walker), *Myospila meditabunda* (Fabricius), *Pararicia pascuorum* (Meigen), *Protophormia terraenovae* (Robineau-Desvoidy), *Scopeuma furcata* Say, and *S. stercoraria* L.

DISCUSSION

Because of the inconsistency in the time period, both daily and overall, that the traps were in operation in the two trapping locations and since they were not in each location on the same days the determination of the statistical significance in the difference between the number of each species caught in each location might not be valid, therefore, no attempt has been made to make these determinations. However, among certain species the difference in the number caught in the two trapping locations was so great that this difference must be indicative of a trend, if indeed not significant. The *Sarcophaga* spp. were taken 84 percent of the time at the beach, as was *Hylemya cilicurra* 69 percent of the time and *Muscina assimilis* 61 percent of the time, while 78 percent of *Muscina stabulans*, 67 percent of *Calliphora vicina*, 61 percent of *Musca*

domestica, and 60 of *Phaenicia sericata* were taken at the kitchen. Differences in other species were not so marked. It would appear to be of particular interest to note that the flies which were taken at the kitchen more frequently than at the beach represented less than 16 percent of the total fly population.

Williams (1954) reported that *Muscina assimilis* was trapped 66 percent of the time at an altitude of 85 feet in New York City, whereas *M. stabulans* was taken only 4.3 percent of the time at this altitude. Other biological differences are to be noted from this study. They exhibit a difference in preference in their choice of local habitat, *M. assimilis* preferring the beach area and *M. stabulans* the environs of the kitchen. The population peak differed by nearly 3 weeks, *M. stabulans* established its highest density of population between July 11 and 20 while *M. assimilis* did not do so until sometime during the first 10 days of August. The population of *M. stabulans* in New York City was about 3 to 1 over *M. assimilis* whereas here in Cheboygan County, Michigan, the situation was reversed with *M. assimilis* dominant by a better than 2:1 ratio.

It is known that *Musca domestica* is not particularly attracted to fish as a bait, as a consequence the number of this species caught is probably not a true index of its population in comparison to other species that find fish more attractive. However, it is true that the house fly was not in evidence in the dining hall until the latter part of July. It is, therefore, felt that the house fly catch is indicative of seasonal distribution and population peak. It can be said that from the standpoint of nuisance value and potential disease transmission, during this summer session at the station, that the house fly was not as important as the many other species which collectively, and in some instances individually, far outnumbered it both out and in-doors.

SUMMARY AND CONCLUSIONS

The population of filth flies attracted to fish was studied at the University of Michigan Biological Station in Cheboygan County, Michigan, during the summer session of 1954. At least 48 species were captured. The percent of the total fly population represented by each species (in some instances by each genus), the population peak, and the choice between kitchen and beach as a local habitat was determined for each species and presented in table 1.

About 84 percent of the total fly population was captured more frequently at the beach than at the kitchen.

Biological differences in habitat and seasonal prevalence between *Muscina assimilis* and *M. stabulans* are brought to light.

The house fly was not as important a pest as were other species during the summer session of 1954.

REFERENCE

WILLIAMS, R. W. 1954—A Study of the Filth Flies in New York City—1953. J. Econ. Ent. 47(4):556-563.

Analysis of a Population of the Tropical Freshwater Shrimp, Atya scabra (Leach)

Rezneat M. Darnell*
Tulane University, New Orleans, La.

During the course of recent investigations on the biology of Mexican streams, the writer secured two samples from a population of the little known tropical freshwater shrimp, *Atya scabra* (Leach). A review of the literature has revealed little information published in this country on the ecology of this crustacean. Ortmann (1894) discussed the distribution of the species, and Allee and Torvik (1927) mentioned its presence in pools of a creek in the Panama Canal Zone. Of the foreign papers, that by Villalobos (1943) is of interest. In this excellent morphological study the collecting method and the habitat of the shrimp in the Rio Necaxa near Coyutla in the state of Vera Cruz, Mexico were discussed. In view of the limited knowledge of the ecology of *Atya scabra* and the uncertain possibility of obtaining additional specimens in the near future, the writer feels justified in publishing this brief population analysis based upon the small samples available.

Acknowledgments.—The author takes this opportunity to thank Dr. Fenner A. Chace, Jr., of the U. S. National Museum for making specific determinations of the shrimp and for criticizing the manuscript. The author is grateful also to Mr. Everts W. Storms, who was his host in Mexico. Original field work for the present study was conducted under a grant from the Tozer Foundation of the University of Minnesota, and further field observations were carried out under a grant from the Tulane University Council on Research. The author wishes to express his appreciation to these supporting institutions.

Habitat

Specimens analyzed in the present study were taken in two collections on April 27, 1950 from the Rio Sabinas, a headwater stream of the Rio Tamesi drainage in southern Tamaulipas, Mexico. The collecting area was Storms' ranch, 7 kilometers northeast of Gomez Farias and about 160 kilometers inland from the Gulf of Mexico at an altitude of 100 meters above sea level.

The habitat of the shrimp was a turbulent riffle, 0-1 meter in depth, with a rock and boulder bottom (fig. 1). Filamentous algae (*Lyngbya* and *Oscillatoria*) made up the only endogenous vegetation. This, however, constituted less than 5 percent of the total vegetation in the riffle, the remainder being composed of exogenous river borne branches, twigs, leaves, and seedpods. Vegetation from the two sources together amounted to 45.1 grams per square meter of riffle bottom. In addition to the shrimp, an abundant and varied gastropod and insect fauna was present. Details of this community will be reported in a later paper.

Throughout six discontinuous months of field work during the winter, spring, and early summer no specimens of this shrimp were observed outside

* Present address: Marquette University, Milwaukee, Wisconsin.

Fig. 1.—Habitat of *Atya scabra* in the Río Sabinas. Rocks were piled to demonstrate the physical composition of the riffle.

the riffle during the daylight hours. At night, however, they were occasionally noted on rocky bottoms in adjacent shallow backwaters, particularly in the vicinity of weed beds.

POPULATION COMPOSITION

A total of 46 specimens were taken from the above-mentioned riffle. These specimens were collected by hand between 11:00 and 12:00 a.m., and the density at the time of collection was estimated to be approximately 10 shrimp per square meter of riffle bottom. Of the total specimens, 28 (or 61%) were males and 18 (or 39%) were females. This difference appears to indicate a preponderance of males in the riffle population, although statistical analysis by the chi-square test demonstrates the difference to be within the expected range of sampling error ($P = .301$). Villalobos (1943) encountered a preponderance of males in both of his large collections of this shrimp taken from a riffle in the state of Vera Cruz. His first collection containing 100 males and 27 females showed a decided statistical significance ($P < .001$) in the sex ratio discrepancy, and his second collection of approximately 400 specimens showed an even greater difference.

From 10:00 to 11:00 p.m. of the day in which the previous collections were made from the riffle, another series was seined from the shallow rocky backwaters 20 to 50 feet upstream from the riffle. This collection contained 5 specimens of *A. scabra* and all were small to moderate sized females. While inconclusive in themselves, the two small samples indicate the possibility that females, and particularly young individuals, occupy marginal habitats around the edges of the riffle (in rocky backwaters) while males and larger females

live principally in the riffle itself. If this is true, then considering the riffle and adjacent marginal areas, there should be a more nearly equal sex ratio than otherwise indicated.

More striking than the apparent habitat discrepancy is the difference in

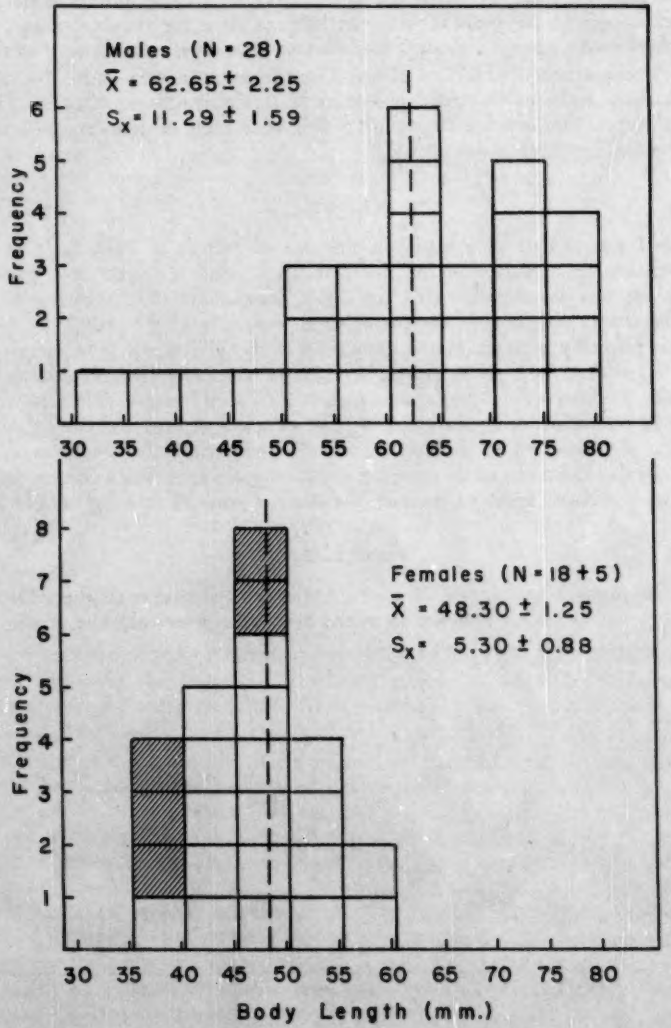


Fig. 2.—Sex and size composition of the population of *Atya scabra*. Clear blocks represent specimens from the riffle; shaded blocks, specimens from the backwater collection. Statistics were computed on the basis of the former only.

mean size of the sexes. As noted in fig. 2, the males ranged considerably larger than the females, and in fact, the mean size of the males was greater than the upper limit of the females taken from the riffle. The standard error of the difference of the means is 1.87 which, on the basis of the "T-test" for small samples, is highly significant ($P < .001$). This size difference can not be explained on the basis of different habitats since the females taken from the backwaters averaged about 5 mm shorter than those taken from the riffle.

A comparison of the sizes of the Tamaulipan specimens under discussion with those collected by Villalobos from Vera Cruz indicates that the latter were larger, *viz.* average length of males, 68.5 mm, of females, 50.0 mm, maximum length of males 94.5 mm.

GROWTH

No observations were made on the rate of growth of individuals in the population or of expansion of the population itself. Proportional growth, however, was investigated (see fig. 3). Comparison of the regression of cephalothorax length on total body length reveals a slight sexual difference which gradually becomes more pronounced as the individuals grow larger. At the larger sizes the females possess a relatively shorter cephalothorax than the males. In other words, the females possess a relatively longer abdomen, which may be correlated with production of large numbers of eggs and the ovigerous habit. As indicated in the section under reproduction, there appears to be considerable mortality in the crowded developing embryos which in turn might act as a selective agent to increase the surface available for egg attachment.

FOOD HABITS

The stomach contents of 20 of the specimens collected from the riffle and all 5 of the specimens obtained from the backwaters were examined under the

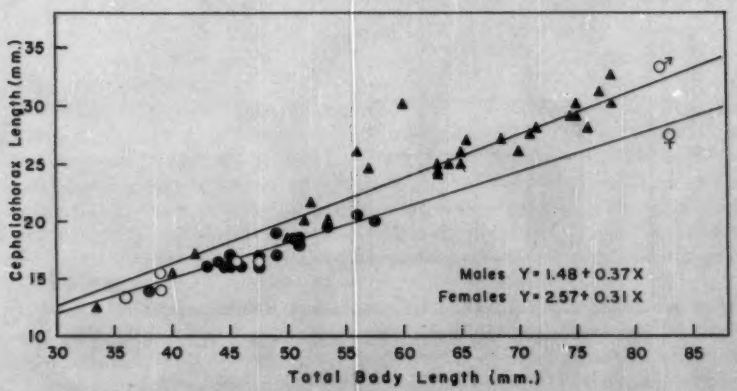


Fig. 3.—Comparison of the relationship between cephalothorax length and total body length in males and females. Solid symbols represent riffle collected specimens; open symbols, backwater specimens. Computations were made on the basis of all specimens.

TABLE 1.—Occurrence of food items in stomachs of 24 specimens of *Atya scabra* containing food. One additional stomach was empty.

Food Item	Percentage of stomachs containing food item	Percentage of total food volume
Unident. detritus	100.0	91.3
Plant remains	100.0	6.9
Arthropod remains	45.9	1.0
Filamentous algae		
Oscillatoria sp.	4.2	All others < 1.0
Mougeotia sp.	95.8	
Spirogyra sp.	4.2	
Diatoms		
Meridion (?) sp.	25.0	
Rhoicosphenia sp.	20.8	
Cocconeis sp	4.2	
Navicula spp.	100.0	
Pinnularia sp.	12.5	
Gyrosigma sp.	4.2	
Cymbella sp.	62.5	
Surirella sp.	4.2	
Unident. diatoms	37.5	
Scenedesmids		
Scenedesmus sp.	4.2	
Desmids		
Cosmarium sp.	83.3	
Micrasterias sp.	8.3	
Hyalotheca sp.	4.2	
Desmidium sp.	66.7	
Protozoa		
Euglypha sp.	4.2	

binocular microscope (45X). Slides were prepared from each of the stomach contents and examined under the compound microscope (645X). The percentage of each of the major food items encountered was estimated, and all identifiable items listed. This information is summarized in Table I.

Only one of the stomachs was devoid of food material. Of the remaining 24, each contained a large quantity of unidentifiable detritus and some plant remains, mostly bits of leaves. About half of the stomachs also contained arthropod remains, including antennae and other appendages of *Atya scabra* and heads, antennae, and appendages of insect larvae and naiads. In most cases these appeared to be bits of cast-off exoskeletons, but in at least one case the insects probably were eaten alive. A variety of algae was encountered, and these were undoubtedly from three sources, upstream (represented particularly by *Navicula* spp. and *Pinnularia* sp.), weed beds (*Spirogyra* sp., desmids, and epiphytic diatoms), and the local riffle (*Oscillatoria* sp.). A single protozoan (*Euglypha* sp.) was found.

Since the stomachs contained little *Oscillatoria* and no *Lyngbya* which were abundant on the exposed rocks, it appears that these shrimp were not feeding from the uppermost rocks but remained at the lowermost levels, con-

suming bits of detritus and other incidental material which filtered through to the bottom of the riffle.

Furthermore, even though large numbers of immature insects were present in the riffle, these formed no major part of the diet of the shrimp. During the daytime individuals were never encountered outside the riffle, but during the night they were occasionally seen in shallow backwaters. The specimens collected from the backwater contained large numbers of *Cosmarium* sp. and other desmids and small numbers of *Navicula* spp. indicating that they were probably feeding out of the main current of the riffle near the weed beds.

REPRODUCTION

Villalobos (1943) found that females collected in March and November carried large numbers of small eggs, and he stated the belief that they are in this condition at all seasons of the year. Unfortunately, no information was included on the relative percentages of ovigerous to non-ovigerous females to aid in determining a possible seasonal peak in breeding.

In the present study, 4 (or 17%) of the 23 females taken in late April were ovigerous. The eggs of 3 of the females showed no signs of development and must have been laid shortly before capture. The eggs of the fourth female showed considerable development, and deeply pigmented eyes were present. Ocular micrometer measurements of 20 of the largest eggs from each ovigerous female revealed the average length of the mature eggs to be 0.84 mm. For comparative purposes ocular micrometer measurements were made on 20 of the largest eggs in the gonads of 13 non-ovigerous females (Table 2).

TABLE 2.—Data on reproduction in 17 female specimens of *Atya scabra*. No attempt was made to determine the number of eggs in non-ovigerous females.

Body Length (mm)	Egg Size (mm) Av.	Max.	Number of Eggs	State of Embryonic Development
		Ovigerous females		
57.5	0.84	0.89	8,000	no noticeable development
50.5	0.86	0.89	1,111	pigmented eyes
47.5	0.79	0.89	1,865	no noticeable development
43.0	0.87	0.89	746	no noticeable development
		Non-ovigerous females		
53.5		<0.05	not counted	
51.0	0.61	0.67		
47.5	0.71	0.89		
46.0		<0.05		
45.5	0.69	0.78		
45.5	0.67	0.78		
45.0	0.59	0.67		
44.5	0.48	0.56		
44.0	0.74	0.89		
39.0	0.87	1.00		
39.0	0.69	0.78		
38.0	0.38	0.56		
36.0	0.72	0.89		

The smallest non-ovigerous female with eggs large enough to be considered mature was 39.0 mm in body length. This may be taken tentatively as the smallest size at sexual maturity. Of the females which had attained this size, two showed what appeared to be recently spent ovaries (developing eggs less than 0.05 mm), and only one appeared to have nearly ripe eggs (0.87 mm). The eggs of the other females showed no particular grouping which might indicate a seasonal peak of breeding, and above 39 mm there exists no obvious correlation between body length and egg diameter. This evidence aids in confirming the belief of Villalobos that breeding takes place during most of the year, but further studies will be necessary to establish details of seasonal breeding intensity and minimum size at sexual maturity.

Eggs of the ovigerous females were counted (estimated on a partial count of 2,500 in the case of the largest female), and the results indicate an approximate logarithmic relationship between body size and number of eggs carried by the females with undeveloped eggs. If this relationship tenuously based on only three specimens, is correct, the 50.5 mm female with developed eggs should have carried approximately 3,000 eggs rather than 1,111. In other words, about 60 percent mortality is indicated for a group of eggs which had reached the eye pigment stage.

MORTALITY

The only predation of *Atya scabra* encountered consisted of a single juvenile specimen consumed by a young (69 mm standard length) individual of *Cichlasoma steindachneri*. This predaceous cichlid was the only fish observed to feed in the riffle. Other potential natural enemies of *Atya scabra* are the large palaemonid shrimp, *Macrobrachium carcinus*, and the fishes, *Gobiomorus dormitor* and *Ictalurus australis*. These three species would be particularly dangerous to individuals living in marginal habitats, especially at night when *Atya scabra* apparently forages in shallow backwaters away from protection of the riffle.

DISCUSSION

The existence of a population of *Atya scabra* in the headwaters of the Rio Tamesi system is of interest since this apparently represents the northernmost locality from which the shrimp has been recorded. Bouvier (1925) and Oliviera (1945) stated the distribution of this species as Mexico, Central America, Panama, Columbia, Venezuela, Brazil, the Antilles (Cuba, Haiti, Jamaica, Dominica, Martinique, Trinidad, and Tobago) as well as West Africa, Australia, and New Caledonia. From a zoogeographic standpoint this shrimp is of tropical origin and constitutes but one of many faunal elements in the Tamesi headwaters of similar affinities. Of the tropical species available, however, *A. scabra* is one of the few which utilize the boulder riffle as the primary habitat.

The apparently continuous breeding season of this tropical species merits additional consideration. Most of the published information on duration and seasonal intensity of breeding relates to temperate species where rather definite seasonal breeding may generally be correlated with annual changes in temper-

ature, rainfall, or light intensity. In headwater streams of eastern Mexico sharp seasonal delimitation has been noted in the hydrographic climate in conjunction with the annual moisture cycle. This is related only incidentally to temperature and primarily to turbidity, volume, and rate of flow of the waters as will be demonstrated in a later paper. It might be expected that marked cyclic environmental changes would be reflected in the seasonal breeding intensity of the species, but the present study has not borne out this idea. Further studies particularly of a seasonal nature on the populations of tropical species are needed to place present information in proper perspective.

SUMMARY

The primary habitat of *Atya scabra* in the Rio Sabinas was shown to be the boulder riffle where there was an apparent numerical preponderance of males over females. Juveniles and some adult females appeared to occupy marginal habitats around the edges of the riffles, and nightly forages into shallow backwaters were noted. Males were demonstrated to grow larger than females and to possess shorter abdomens which may be correlated with the ovigerous habit of the females. Food of this shrimp consisted mainly of exogenous detritus gathered from the bottom of the riffles. Gonad analyses substantiated Villalobos' belief that breeding takes place throughout most of the year. Egg counts were given for ovigerous females and some developmental mortality was indicated.

REFERENCES

ALLEE, W. C. AND M. TORVIK 1927—Factors affecting animal distribution in a small stream of the Panama rain forest in the dry season. J. Ecol. 15:66-71.

BOUVIER, E. L. 1925—Recherches sur la Morphologie, les Variations et la Distribution systématique des Crevettes d'eau douce de la famille des Atyidés. Encyclopédie Entomologique IV.

OLIVIERA, L. P. H. DE 1945—Verificacão da existência de *Atya scabra* Leach, camarão dágua doce de família Atyidae, crustacea, no nordeste do Brasil. Mem. Inst. Osw. Cruz, Rio de J. 43(2):177-190.

ORTMANN, A. E. 1894—A study of the systematic and geographical distribution of the decapod family Atydae (Kingsley). Proc. Acad. Nat. Sci. Philadelphia. 397-416.

VILLALOBOS, A. 1943—Estudio morfologico de la *Atya scabra* (Crust., Deacp.). Thesis, Universidad Nacional de Mexico. March, 1943.

Studies on the Morphology and Biology of Acetodextra amiuri (Stafford) (Trematoda: Heterophyidae)[1]

Kenneth W. Perkins
Purdue University, Lafayette, Indiana

Acetodextra amiuri is a heterophyid trematode which parasitizes fishes, especially Siluridae. *A. amiuri* is of unusual interest in several respects. In structure it is typical of the Heterophyidae and yet it is a parasite of fishes, whereas other members of that family, as restricted by Price (1940), occur in birds and mammals. This situation is further evidence that closely related trematodes may not necessarily occur in related hosts, although the type of host has been stressed in taxonomy by some investigators. *A. amiuri* is unusual also in respect to its localization in the definitive host. All other adult trematodes in the superfamily Opisthorchioidea live in the digestive tract or its appended organs whereas *A. amiuri* does not. While this trematode was known for some time only from the air bladder of catfishes, it is evident from the present study that the ovaries are the more important site. This trematode may be histozoic or even cytozoic, as young worms were observed within the eggs of the host. This unusual site of infection in the definitive host is not only unique in the Opisthorchioidea but has been reported for no other adult digenetic trematode. Thus *A. amiuri* presents a number of problems differing from those encountered in the investigation of any other member of its family. Among these problems are 1) the method by which the definitive host becomes infected, 2) the effects on reproduction of the host, 3) the fate of the parasite in males of the definitive host species, and 4) the means whereby the eggs of the parasites escape to continue the life cycle.

Historical Review

Acetodextra amiuri was first described by Stafford (1900) as *Monostomum amiuri* from the air bladder of *Ameiurus nebulosus*. He referred to the species as "very soft bodied, inactive creatures" which he allocated to the genus *Monostomum* through an error in the interpretation of the ventral sucker as an "extremely muscular vagina." Pearse (1924) redescribed the worm, and erected for it the genus *Acetodextra*. He found adults in the swim bladders of *Ameiurus natalus, A. melas* and *A. nebulosus* and young encysted forms in the liver of *Schilbeodes gyrinus*. Hunter and Hunter (1932) were the first to report the species from the ovary, that of *Ameiurus nebulosus*. Mueller and Van Cleave (1932) again described the fluke from the swim bladder of about

[1] Based on a thesis submitted to Purdue University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. This study was supported by a Fellowship of the Purdue Research Foundation, 1952-53, and was directed by Prof. R. M. Cable.

15% of the bullheads from Oneida Lake, New York. Bangham and Hunter (1939) gave a second record of the parasite from the ovary of a catfish, in this instance, *Ictalurus punctatus*. Recently, Coil (personal communication) has reported finding the worm in the ovary of *Cottus bairdii*, the only host thus far known that is not a silurid fish.

The taxonomic position of *Acetodextra* remained in doubt until 1931 when Van Cleave and Mueller placed it in the Heterophyidae. In a later paper, these authors (Mueller and Van Cleave, 1932) discussed the family and the interesting genital complex of these worms. Mueller (1934) redefined the Heterophyidae to include parasites of fishes as well as those of birds and mammals so that *Acetodextra* would fall into the family characterization.

Witenberg (1929) first proposed that the Heterophyidae be combined with the Opisthorchidae to form a new superfamily, the Opisthorchioidea. However, this name had been used previously by Faust (1929) to designate a group containing only the Opisthorchidae as opposed to the superfamily Heterophyoidea, which contained the Heterophyidae, Microphallidae and Lecithodendriidae. Faust used the symmetry of the miracidium as a character distinguishing these two superfamilies. According to him the miracidium is symmetrical in the Heterophyoidea and asymmetrical in Opisthorchioidea. He also considered the flame cell pattern to be a character of the superfamily value.

Ciurea (1933) followed Faust's superfamily designations, but revised the superfamily Heterophyoidea, including in it a new family, the Cryptogonimidae, in which the uterus is largely posttesticular as contrasted with the Heterophyidae. He rejected the Lecithodendriidae because of the extent and distribution of the vitelline glands. Vogel (1934), using cercarial types as a basic character, suppressed Faust's Heterophyoidea and combined under the new name Opisthorchioidea, the Heterophyidae and Opisthorchiidae. In combining these groups Vogel pointed out that the *asymmetrical* miracidium which Faust described is very similar to that of the heterophyid, *Cryptocotyle lingua*, as drawn in lateral view by Stunkard (1930).

Price (1940) has given the most recent review of the superfamily Opisthorchioidea. Using the cercarial type as a basis for relationship, he placed in the Opisthorchioidea, the Opisthorchiidae, Heterophyidae, Cryptogonimidae and Acanthostomidae, all of which have either the pleurolophocercous or the parapleurolophocercous type of cercaria. The last two families are separated from the Heterophyidae largely on the basis of the shape and extent of the excretory bladder. Cable and Huninen (1942) expressed doubt that this character is of family value and suggested that the Cryptogonimidae and the Acanthostomidae probably should not be retained as distinct families. Baer (1943) proposed the Pachytrematidae and Ratziidae to rank with the Opisthorchiidae in the superfamily but the validity of this arrangement may be questioned in the absence of information concerning life histories.

Price (1940) listed studies concerning opisthorchioid life histories. Since that time, several additional cycles have been traced experimentally and information bearing on others has been reported. In the Opisthorchiidae are the life histories of *Metorchis orientalis* and *M. tainwanensis* by Tao (1948), *Phocitremoides ovale* by Martin (1950a), *Ratzia joyeuxi* by Buttner (1951, 1952) and *Opisthorchis tonkae* by Sillman (1953). In the Heterophyidae,

Martin has added the life histories of *Euhaplorchis californiensis* (1950b), *Parastictodora hancocki* (1950c) and *Pygidiopsoides spindalis* (1951). Also further information concerning the cycle of *Metagonimoides oregonensis* has been given by Burns and Pratt (1953). In the Cryptogonimidae, Komiya and Tajimi (1940) have traced the life cycle of *Exorchis oviformis* and Cable and Hunninen (1942) that of *Siphodera vinaledwardsii*.

In all known life cycles of opisthorchioid trematodes, the cercaria is of the pleurolophocercous or parapleurolophocercous type except in *Centrocestus armatus* whose larva, according to Yamaguti (1938), lacks a caudal fin, but is otherwise similar to known opisthorchioid larvae. Cable (1952) has postulated yet another type of larval opisthorchioid, namely a magnacercous type in which the tail lacks fins altogether and may be greatly enlarged and pigmented. In one of the species which he found in Puerto Rico, the tail is even used to unite large numbers of the larvae in zygocercous (*Rattenkönig*) clusters.

MATERIALS AND METHODS

Catfish were obtained from the Wabash River, killed and examined immediately to obtain parasites and host tissue in the best condition. Although the entire fish was examined, particularly close scrutiny was made of the ovary and swim bladder from both of which *A. amiuri* has been reported by previous workers. After the ovaries were separated and measured, one was fixed for histological examination while the other was dissected and examined for flukes. If the parasites were mature, they were usually either fixed for subsequent examination or used as a source of eggs for later use; young specimens were studied alive under cover glass pressure to observe the excretory system and other structures which are either difficult to see in stained material or obscured by eggs in the uterus of older worms. Fixatives used were FAA and Schaudinn's fluid. Whole mounts and sections were stained with hematein and fast green was used to counterstain sections.

Smears were made of the testes by transferring the adult worm to a clean slide with as little liquid as possible and then piercing the body in the region of each testis with a fine needle. The material which exuded from the worm was then spread slightly and the slide was immediately immersed in hot (70°C) Schaudinn's fixative or Flemming's solution, either with or without acetic acid. Such smears were stained with Heidenhain's hematoxylin. Schaudinn's fixative gave better results than did either modification of Flemming's solution.

Ovarian tissue of the catfish was fixed in Carnoy-Lebrun's fluid for about four hours, dehydrated with ethyl and isopropyl alcohol, imbedded in paraffin and sectioned at 6 microns. This material was stained in Harris' hematoxylin using either fast green or Biebrich's scarlet as a counterstain. Ovarian cysts were treated in the same manner. When gravid worms were placed in a finger bowl of tap water their eggs were quickly voided. Thus large numbers of eggs were obtained and *cultured* in running water.

In efforts to find the larval stages of *A. amiuri*, snails were collected from various localities and isolated for emerging cercariae. As it was possible that the larvae might not emerge from snails handled in this manner, numerous mollusks were cracked and examined. When a pleurolophocercous cercaria was

found, the infected snail was isolated and every available fish and amphibian was exposed to infection.

OBSERVATIONS AND DISCUSSION

Morphology of the adult (figs. 1-3).—The worms are linguiform and flattened, with a posterior notch in the region of the excretory pore. When young, they are a dull white but as they become gravid, eggs are visible through the body wall, imparting a brown color to the regions occupied by the uterus. Mature worms measure from 2.3-4.1[2] (av. 3.2) in length and 0.57-1.43 (av. 1.14) in width. The cuticle of the parasite, although relatively thick (0.013), is poorly defined, sometimes having an almost ragged appearance. Imbedded in it are very small obscure spines, 0.015 long, arranged in quincuncial pattern. They are distributed over the entire anterior two-thirds of the body, diminishing in number as the posterior limit of their range is approached. The spines arise at the basement membrane of the cuticle and are directed posteriorly at an angle of about 45° to the body surface, ending just above the surface of the cuticle, and typically bearing a very small hook at the distal tip. The species was originally described as being aspinose; this error was corrected by Arnold (1934) however, and is verified in the present study.

As is often the case with adult trematodes living outside the digestive tract, *A. amiuri* has poorly developed musculature and a vesicular, very loosely organized parenchyma, elements of which are displaced with movements of the worm. Several small spherical to ovoid nuclei, 0.008-0.009 in diameter, are dispersed throughout the parenchyma. There also is a smaller number of large prominent nuclei which measure about 0.012 in diameter and contain a large nucleolus, 0.004 in diameter, and several darkly staining chromatin granules; the cytoplasm surrounding these nuclei stains a deep blue with hematein, making the cell the most conspicuous element of the parenchyma. To a depth of 0.04 below the cuticle, the parenchyma is considerably denser than elsewhere and contains a large number of spherical nuclei, 0.008 in diameter, each with a single nucleolus.

The oral sucker is nearly spherical in shape, measuring 0.105-0.195 (av. 0.168) in diameter; the mouth is directed slightly ventrad. A prepharynx is absent; the pharynx measures 0.087-0.150 (av. 0.129) in length. The esophogus is 0.07-0.33 (av. 0.22) long and joins the intestine about midway between the oral sucker and the genital pore. The ceca are long, terminating about 0.25 from the posterior end of the body, and are lined with an epithelium of irregular thickness.

The ventral sucker measures 0.164-0.315 (av. 0.26) in diameter and lies about one-third of the body length from the anterior end. It is displaced to the right and is very deeply imbedded in the parenchyma, actually lying closer to the dorsal than the ventral surface of the body in most specimens. Anterior and somewhat to the left of the ventral sucker is the gonotyl which measures 0.06-0.13 (av. 0.089) in diameter and when retracted lies in a muscular sac a little smaller than the ventral sucker. This sac is an extension of the large ventro-genital pit which receives also the opening of the ventral sucker. The

[2] All measurements are in millimeters.

opening from the ventro-genital pit to the outside is seen distinctly by focusing on the ventral surface of the worm. Its shape varies with the degree of contraction of the specimen and the extent to which the gonotyl is protruded; usually, however, the opening is elongate oval or pyriform. Although in heterophyids this opening has often been called the genital pore, and the ventro-genital pit the genital sinus or atrium, the author's observations support those of Witenberg (1929) and Cable and Hunninen (1942) and further emphasize that such terminology is inaccurate and confusing. The opening corresponding to the genital pore in less modified trematodes and hence the true one, opens into the ventro-genital pit between the ventral sucker and the gonotyl. From this pore there extends inward a very short common duct sometimes called the hermaphroditic duct, but actually corresponding to the genital atrium of other trematodes. This divides almost immediately to form the ejaculatory duct and a thin-walled metraterm. The ejaculatory duct passes obliquely posteriad nearly 0.2 and then enlarges slightly to form an elongate *pars prostatica*. This is divided into two distinct regions, the anterior of which is surrounded by small spindle shaped cells about 0.03 long and containing deeply staining nuclei. The second or more posterior portion is longer than the first and receives the ducts of extremely numerous and prominent prostate cells. These cells and their ducts are scattered over a wide area (fig. 1), extending to and partly around the ceca. Closely joined to the posterior end of this region is the seminal vesicle, which is thin-walled throughout, shows no indication of being bipartite, and is very large, measuring 0.45-1.35 (av. 0.93) long and 0.105-0.195 (av. 0.15) in width. The vesicle extends as a sinuous tube from the left side of the intercecal region to the anterior margin of the ovary where it receives the vasa efferentia. If a vas deferens is present, it is extremely short. The vasa efferentia pass almost directly posteriad to join the testes which are situated side by side at the posterior end of the body. The testes are extremely variable in shape and range in length from 0.510-1.105.

The ovary is irregularly lobed, measuring 0.240-0.585 (av. 0.387) in diameter. It lies somewhat posterior to the middle of the body and is adjacent to the ventral surface. The oviduct leaves the antero-dorsal region of the ovary, extends dorsally for a short distance, and then turns to the left where it receives first the duct from the seminal receptacle and then the common vitelline duct. After continuing a short distance anteriorly, the oviduct enlarges to form the oötype and the tract then expands as the uterus. In young worms the beginning of the uterus can be seen to turn posteriorly almost immediately and pass over the ventral surface of the testes; then it bends and extends anteriorly on the right side of the body to the ovarian level. There the uterus crosses obliquely to the left side of the mid-line and returns to the right as the metraterm which joins the male duct at the genital atrium. In large mature worms, the uterus becomes sacciform and its path cannot be followed. Although the metraterm does not enlarge, the terminal portion of the uterus in gravid specimens extends pouch-like into the intercecal region anterior to the genital pore.

The seminal receptacle lies slightly to the left of the ovary and may be either anterior or posterior to that organ. The receptacle is 0.150-0.405 (av. 0.274) in diameter, the size varying with the sperm content. There is a very

short seminal duct extending from its midventral surface, and Laurer's canal leads away from the receptacle at the same level but farther to the left and dorsally around the seminal receptacle and uterus, opening on the dorsal surface about 0.15 to the left of the median line, and near the level of the posterior edge of the ovary. The vitellaria are extracecal and extend from the ventral sucker level to or very slightly beyond the posterior end of the ceca. The vitelline ducts originate at a level slightly posterior to the ovary and are ventral to the ceca as they pass medially to unite as the common vitelline duct dorsal to the ovary. The common duct extends directly anteriad to join the oviduct. The oötype is surrounded by a very large Mehlis' gland. No eggs have been found in the oötype, but very young ones with colorless shells are present in the beginning of the uterus. Each of these young eggs contains four or five yolk cells and the maturing ovum with the enclosed sperm. In proceeding away from the öotype, eggs in the uterus show progressive stages in maturation and in old degenerating worms, the eggs filling the enormous uterus contain miracidia.

The excretory bladder is Y-shaped with very short arms. The bifurcation occurring between and near the anterior end of the testes (fig. 3). Each arm tapers very gradually as it passes anterolaterally, but a few specimens show a localized narrowing where the main tubules begin. This constriction was never seen in the living specimens but is sometimes visible in stained whole mounts of very young worms. Each main excretory tubule passes anteriorly close to its side of the body and extends to the level of the esophagus; there the tubule turns posteriorly and extends almost to the vitellaria where it receives an anterior and a posterior collecting tubule. Each of these tubules is joined by three groups of flame cells having four flame cells per group. Thus the excretory formula is $2[(4+4+4)+(4+4+4)]$. Each flame cell group is connected to the secondary tubule by a short common duct. The pattern given in fig. 3 is for young worms (less than 1 mm long) in which the duct system is very much less convoluted than in old specimens. In large worms, the excretory tubules lie so close together between the gut and the sides of the body and their convolutions are so entangled that the excretory system is extremely difficult to follow.

Description of the Egg and Miracidium (fig. 4).—The eggs of *A. amiuri* are rather uniform in size and shape. They measure 0.041-0.045 in length and 0.022-0.024 in width, are somewhat pyriform in outline, and possess a distinct operculum. There usually is an antopercular excrescence of shell material. When extruded from living adult worms in the manner described below, each egg contains an embryo in an advanced stage of cleavage. In such eggs, the miracidium develops within a period of two weeks and will remain alive for at least two months without any apparent changes. No evidence of hatching was observed, thus implying that the embryonated egg must be eaten by the molluscan host as in other opisthorchioids. Most observations of the miracidium have been made through the egg shell. Since that larva is studied to best advantage when free of the shell, attempts were made to release it. Although a few free miracidia were obtained by exerting pressure on the egg, they were always injured and disintegrated quickly. On one occasion beating of the cilia for a very short time was observed. The larva, when within the egg, is enclosed

in a distinct vitelline membrane, which usually contains a large vacuole pressing the miracidium to one side, and several yolk masses of various sizes. For the most part, this membrane is applied closely to the shell and sometimes has what appears to be fine folds or wrinkles. The miracidium is 0.039 to 0.043 long and about 0.01 wide, and is covered with very long cilia which were never observed to move within the egg shell, although Brownian movement of minute granules near them gave the appearance of ciliary movement at times. However, periodic contractions of the miracidium were observed and occurred rather frequently, especially in specimens exposed to intense light. Structures which could be seen within the miracidium (fig. 4) included the *primitive gut*, a single cephalic gland, the pair of flame cells, a large spherical mass visible just posterior to the cephalic gland of some specimens, and several small spherical bodies in the posterior region. An eye spot is lacking.

The miracidium of *A. amiuri* is very similar to that described by Faust *et al.* (1927) and by Vogel (1934) for other opisthorchioids, the chief difference being the size and shape of the cephalic gland, and the disposition of its duct. In the miracidia of *Clonorchis sinensis* and *Opisthorchis felineus*, the cephalic gland is an elongate structure lying along one side of the larva with the duct crossing to the other side and then extending anteriorly. The flame cells were described in both cases as being close together on one side of the larva. In the miracidium of *A. amiuri*, the cephalic gland is comparatively short and triangular in shape and its duct passes more directly to the anterior end. Usually the flame cells are seen as described above, but are situated at definitely superimposed levels as determined by careful focusing. In the miracidium of *O. felineus*, Vogel (1934) described the primitive gut as containing a single nucleus, while in *A. amiuri*, there are at least four or five minute structures which may be nuclei. The large granular body found in the middle region of the miracidium may correspond to the ganglionic mass described for larger species, and the several smaller bodies found near the posterior end probably are germinal cells.

It was on the basis of an apparent structural asymmetry that Faust (1929) stated that an asymmetrical miracidium was diagnostic of the Opisthorchioidea. Since the miracidia of *A. amiuri* invariably present the view shown in fig. 4a when eggs are mounted in the fresh state without pressure, and since the miracidia of trematodes in the other families show a somewhat similar arrangement and asymmetry of parts when seen in side view, it seems quite possible that the miracidia of the opisthorchids are not actually asymmetrical when seen in dorsal aspect. In miracidia, the excretory system is bilaterally symmetrical, as a rule with the flame cells laterally situated. The fact that they are placed to one side and superimposed on one another (fig. 4a) would suggest that this is a lateral rather than a dorsal view. For this reason, attempts were made to manipulate the eggs so that the flame cells were at the same level of focus. When this was accomplished they were found to be widely separated (fig. 4b) and close to their respective sides of the larva. However, when the miracidium was in this position, the cephalic gland appeared to be asymmetrical in shape with its ducts extending along one side of the primitive gut. When the egg was manipulated so that the anterior part of the gland was median in position, the duct always curved laterally before enlarging as the cephalic

gland. However, in order to handle the eggs in this manner, it was necessary to use considerable coverglass pressure and in view of the shape of the egg, it is quite possible that the miracidium may have become twisted. This would account for the fact that a symmetrical arrangement of the flame cells and the cephalic gland with its duct in a median position were not observed simultaneously.

GAMETOGENESIS

SPERMATOGENESIS

The testes of *Acetodextra amiuri* provide excellent material for the study of spermatogenesis. Stages float freely in a fluid within the testes and smears of the developing germ cells are easily obtained. Such smears contain large numbers of all stages in spermatogenesis except the primary and secondary spermatogonia which adhere to the tunic of the testis. The description of spermatogenesis given below is based on both smears and sectioned material, although most of the photographs are of smears. For this reason, the cells in several figures are somewhat distorted due to flattening of the spherical clusters which accordingly appear larger than when seen in sectioned material. In *A. amiuri* the diploid chromosome number is 12.

The various stages of spermatogenesis are arranged in the usual manner in the testes of the parasite, i.e. with the primary and secondary spermatogonia near the testis wall and the later stages more or less progressively farther toward the center. However, because of the loose, almost fluid content of the testes, the later stages tend to become mixed as a result of the body movements of the mature worms.

Primary Spermatogonia.—The primary spermatogonia are small, measuring 0.0076 in diameter. The oval nucleus is very distinct, measuring about 0.0045 by 0.006 and contains a small karyosome (0.002). Several primary spermatogonia were found undergoing mitosis in sectioned specimens (fig. 5); all were in late anaphase and the chromosomes could not be counted.

Secondary Spermatogonia.—The secondary spermatogonia (fig. 6) are so similar to the above stage that they can be distinguished only by the fact that they are always paired, appearing as two nuclei in a cytoplasmic mass with no evidence of separation into two cells. No division figures were seen for this stage which was never observed in smears.

Tertiary Spermatogonia.—This is the first stage which occurs in numbers in the smears. It consists of four cells connected by a fine protoplasmic strand (fig. 7). Fig. 8 shows tertiary spermatogonia in division; two of the cells clearly have the diploid number of chromosomes.

Primary Spermatocytes.—With the division of the tertiary spermatogonia, the primary spermatocytes are formed. These are still united so that there are now eight cells in each group. This stage was extremely abundant in the smears, and many clusters in nuclear division were observed. In the resting phase (fig. 9) the nucleus stains evenly and there are basophilic bodies in the cytoplasm. These inclusions are very similar in appearance and position to the mitochondria described by Dingler (1910) and Yosufzai (1952). The chromatin mate-

rial in the nucleus begins to form into threads (fig. 10) and then very delicate leptotene fibers appear (fig. 11), which have several node-like thickenings along them. Presumably synapsis occurs at this time and although the leptotene threads could not be counted in the smears, some cells in the sectioned material showed a distinct diplotene. Soon after the appearance of these threads, all indication of the nuclear membrane disappears and the chromosomes condense to the typical bivalent form (fig. 12). As is easily seen, the number of bivalents at this stage is six, with four small rounded chromosomes and two larger V- or U-shaped ones, which are about 0.008 long and 0.0015 thick. The beginning of metaphase is evident in the larger chromosomes in which the formation of loops is frequently observed. The bivalents then divide (figs. 13 and 14) without the formation of an evident spindle, and the secondary spermatocytes are formed.

Secondary Spermatocytes.—In the sixteen-cell groups which result from the first maturation division, the cells are smaller than those in the primary spermatocytes. In this case there is a distinct karyosome in the nucleus (fig. 15). None of the phases preparatory to the division of the secondary spermatocyte was observed. The chromosomes condense and are distinctly smaller than those seen in the previous stage, the two large ones measuring about 0.0045 long and 0.0008 thick (fig. 16). Individual chromosomes were seen best in sectioned material. Division of each chromosome is evidently equational and without the formation of a spindle that could be seen (fig. 17).

Spermatids and *Spermatozoa.*—The resting nucleus of the spermatid is very distinct and has an eccentric karyosome (fig. 18). The nucleus becomes very dense and elongates with an accompanying attenuation of the cytoplasm which is drawn to a fine point at the free end (fig. 19). In fig. 20, the nucleus has become longer and a few filamentous cytoplasmic strands may be seen. The heads of the mature sperms are at first tangled in a mass with the long tails tending to lie parallel and in a group (fig. 21). The sperms become separated, however, and individual ones were abundant throughout the smears (figs. 10 and 11). In sections counter stained with Biebrich's scarlet, there was a distinct difference in the staining characteristics of regions of the sperm; the end presumed to be the head stained intensely with the nuclear stain, whereas the long filamentous tail portion took up the acidophilic stain. It will also be observed (fig. 20) that there is no evidence of a residual body of cytoplasm as has been described for other species; instead, the cytoplasm as well as the nucleus of the spermatid contributes to the formation of the sperm.

OOGENESIS

Oögonia and *Primary Oöcytes.*—Around the periphery of the ovary in the mature parasite there is a zone of oögonia which are relatively small (0.007 in diameter) and have very little cytoplasm (fig. 22). The spherical nuclei of these cells are somewhat variable in size, ranging from 0.004 to 0.006 in diameter, and contain a fine chromatin network and a distinct eccentric karyosome. Several dividing oögonia were found in the late anaphase, but none was seen in earlier phases of division. The chromosomes were so packed together in these cells that they could not be distinguished individually.

Primary oöcytes passing through a premeiotic phase are found in a narrow area just internal to the oögonia. The chromatin material in these cells first forms into a typical spireme, then the leptotene thread breaks into a number of pieces. The number of chromosomes could not be counted at this stage since they are not polarized and are somewhat entangled. They are finer in appearance than in later stages and appear to be more numerous than the haploid number. Upon further condensation of the chromosomes a distinct bouquet pattern appears (fig. 23), with a large endosome at the base of the loops. In cross sections of the oöcyte in this configuration (fig. 24), twelve ends, i.e. six loops, can be counted. Thus, since the 2n number of chromosomes is 12, there evidently has been synapsis of the homologous pairs. The nucleus of the oöcyte then returns to interphase, though its chromatin is more diffuse than in the gonial cells. The entire central portion of the ovary is made up of such *resting* oöcytes which are very indistinct, the nuclei staining but slightly (fig. 24).

The primary oöcytes near the oöcapt are much more loosely packed than elsewhere and they show a greater affinity for hematein than do other cells in the ovary (fig. 25), even the cytoplasm taking on a blue color. The nucleus is that of a typical interphase with a conspicuous eccentric karyosome, and a distinct network of chromatin. There is no apparent difference between the cell at this point and just after it is enclosed in the egg shell (figs. 26 and 27) except that the very long filamentous sperm is loosely wrapped around the oöcyte in the newly formed egg. Upon penetration of the sperm into the cytoplasm, the chromatin of the oöcyte nucleus condenses (fig. 28) with the formation of six bivalent chromosomes (fig. 29) which are very similar to those found in the primary spermatocyte. The chromatin threads appear to be doubled as they are condensing, again reflecting the bivalent character of the chromosomes in this stage. The chromosomes become aligned along the equatorial plate (fig. 30) and then with the formation of a distinct spindle the bivalents divide (fig. 31); one set of the resulting chromosomes separates from the oöcyte with a small amount of cytoplasm to form the first polar body, which at first is vesicular (fig. 32) although it condenses and appears as a deeply staining nucleus surrounded by a small amount of clear cytoplasm in older eggs (fig. 33). During this maturation division, the sperm becomes progressively shorter and thicker and by the time the first polar body is formed the sperm is only slightly longer than the diameter of the oöcyte and becomes fusiform in shape (fig. 30).

Secondary Oöcytes.—The resting nucleus of the secondary oöcyte is very rarely seen. It can be recognized, however, by the presence of the first polar body. Following interphase the chromosomes again condense and although they are much smaller and more delicate (fig. 34), they are of the same number and shape as in the primary oöcyte. After alignment on the equatorial plate. each chromosome evidently divides mitotically and one set is eliminated in the second polar body (fig. 35). By this time the sperm is extremely compact and forms a small pyriform mass (fig. 34).

Pronuclei and Fertilization.—The female nucleus again returns to interphase with the typical chromatin net and eccentric karyosome. The male nucleus enlarges and becomes vesicular, at first being easily distinguished from

the female nucleus because of its smaller size and its less uniform staining (fig. 36). Finally, however, the two nuclei become indistinguishable and fuse (fig. 37) before the fertilization spindle appears.

Cleavage in *A. amiuri* was not followed. By the end of the maturation process, the shell becomes so impervious and brittle that fixation, staining and sectioning gave poor results.

Gametogenesis has been studied for relatively few trematodes. A review of the earlier work in this field was given by Cable (1931) and more recent literature is reviewed by Yosufzai (1952, 1953). With the exception of the work done by Dingler (1910) who used smears of the testes of *Dicrocoelium lanceatum*, most such studies have dealt with sectioned material which has one serious disadvantage, viz., the necessity of reconstruction except in very thick sections. Gametogenesis as described for various digenetic trematodes differs very little from one species to another, though the diploid chromosome number varies from twelve to twenty or more. *A. amiuri* has chromosomes similar in shape and number to those of *Cryptocotyle lingua* the only other heterophyid for which the number of chromosomes has been reported (Cable, 1931). Since this paper went to press, Van der Woude (1954) has given an excellent account of gametogenesis in *Megalodiscus temperatus*.

There have been several points of discussion concerning the interpretation of various phases of the maturation process. Cable (1931), Anderson (1935), and Willey and Godman (1941) have indicated that in all probability the first maturation division is of the reductional type, i.e. homologous chromosomes are separated in the resultant cells. It is pointed out by Willey and Koulish (1950) that no definite conclusions can be drawn concerning this question at the present time because there is no method of identifying the members of the homologous pairs, or being certain that the first maturation division actually separates them instead of involving equational division of each component within the pair.

The presence of nutritive materials in the gonads has been reported by several authors. Kathariner (1904), Goldschmidt (1908), Gille (1914), and Anderson (1935) have observed degenerating nuclei in the ovaries or oöcytes of the species which they have studied. For the most part these nuclei have been interpreted as abortive oöcytes which contribute to the nutrition of the normal cells. Chen (1937) however, believed that the germ cells are nourished by the body fluids of the worm, while Cable (1931) suggested that degenerating cells found in *Cryptocotyle lingua* are probably derived from yolk cells which resemble oöcytes somewhat. No such degenerating cells were found in the ovary or eggs of *A. amiuri*.

There has been considerable disagreement as to the structure of the mature sperm. Dingler (1910), Woodhead (1931), and Yosufzai (1952) consider that the sperms of the species they have examined consist of both nuclear and cytoplasmic elements as is the case in other groups of animals. All other investigators, however, have indicated that the sperm is composed entirely of nuclear material and that the cytoplasm is left behind as residual masses in the testis. There was no evidence of such residual masses in *A. amiuri;* the entire spermatid elongates and the resulting sperm clearly consists of both nuclear and cytoplasmic elements.

BIOLOGY OF ACETODEXTRA AMIURI

All of the several life histories which have been traced in the superfamily Opisthorchioidea have involved cercariae of either the pleurolophocercous or parapleurolophocercous type. Except for its habitat, *A. amiuri* is a typical member of the superfamily and for that reason, it was expected that the cercaria if found would be much like known larvae in the group. This belief was supported also by remnants of eye spots in the adult and even retention of cephalic gland ducts in the same number and pattern characterizing the great majority of opisthorchioid cercariae, both fresh water and marine. Accordingly an intensive search was made for larvae of that type with the expectation that among them would be a cercaria proving to be the larva of *A. amiuri.*

Over a period of five years, large numbers of every species of mollusk that could be found and which might harbor opisthorchioid larvae were collected. These mollusks included four species of prosobranch snails from the Lafayette area, *Pleurocera acuta, Goniobasis livescens, Campeloma rufum,* and *Amnicola limosa,* and a species of *Goniobasis* from southern Indiana and Kentucky. Also during the course of this study, large numbers of bivalves and pulmonate snails were being used in the laboratory for other investigations during which none was found to be infected with larvae of the type sought. Of over 50,000 prosobranch snails collected and examined, a total of 39, or 0.08%, were found to harbor such larvae. Snails taken in southern Indiana (Clifty and Laughery creeks) and in east-central Kentucky (Cow Bell Creek, Madison County) comprised about 5% of the total number of snails examined and accounted for nearly 60% of the infections found. Thus the mollusks from the Lafayette area showed an incidence of about 0.03%. Two species of pleurolophocercous cercariae were found during this study: (1) *Cercaria vogeli* Cable occurring in both *Pleurocera acuta* and species of *Goniobasis* from all areas investigated, and (2) *Cercaria semicarinatae* Cable and Wheeler, infecting only the species of *Goniobasis* from Kentucky and southern Indiana. No infections were found in *Amnicola limosa* or in *Campeloma rufum.* Experiments with *C. vogeli* and *C. semicarinatae* indicated that neither of these cercariae was the larvae of *A. amiuri.*

Although the intensive effort to determine the life cycle of *Acetodextra amiuri* was not successful, observations which may eventually aid in the solution of the problem were made. One unknown aspect of the life history is the manner in which the immature worms reach the ovary of the catfish. This site is undoubtedly the natural one for the adults of this species and their occurrence elsewhere such as in the swim bladder must be regarded as erratic parasitism. Van Cleave and Mueller (1934) found young worms in the digestive tract and suggests that in reaching the swim bladder of the host the metacercariae excyst in the alimentary tract and migrate to the swim bladder by way of the pneumatic duct. Since the worms are predominantly parasites of the ovary, the pneumatic duct route would be unavailing in reaching that site without penetration of the swim bladder. If this were the route used it would be expected that young worms would be found in the pneumatic duct and bladder of at least some of the many fishes that have been examined, especially those having large numbers of very young worms in the ovary. Such has not been the case. Other routes by which worms may reach the ovary include: (1)

excystment of the metacercariae in the intestine, their penetration, and migration of the young worms, either through the capsule and tissues of the gonad or to that organ by way of the blood stream; (2) migration of excysted metacercariae from the anus, into the urinogenital opening, and then up the oviducts and to the ovaries as claimed for some bladder flukes; and (3) direct penetration of the definitive host by the cercariae and their migration to the ovary, thus eliminating a second intermediate host in the life cycle.

For the definitive host to become infected by direct penetration of cercariae would be a decided innovation in the life history of an opisthorchioid, since as a rule, its cercaria encysts in fishes or rarely amphibians. These vertebrates are normally eaten by large catfish which harbor *A. amiuri* and it seems likely that they may obtain the parasite in that manner. The occurrence of *A. amiuri,* however, in fishes such as small bullheads and *Cottus bairdii* suggests a possibility that the trematode may not have a second intermediate host, but that instead, this species may become sexually mature in what corresponds to the second intermediate host of other heterophyid trematodes. *A. amiuri* is unlike all other opisthorchioid trematodes in that it does not localize in the intestine or biliary passages, but is a parenteral parasite and the very young worms may even be cytozoic, living within the developing egg of the host (fig. 38). Furthermore such worms are little larger than the cercarial body of many species of opisthorchioids and contain seven distinct pairs of cephalic gland ducts (fig. 2), the number most commonly observed in cercariae of this group. Certainly if *A. amiuri* has a second intermediate host there can be very little growth of the metacercaria in that host and little modification of the cephalic glands. It is true, however, that Vogel (1934) observed the retention of the cephalic glands by the young adult of *O. felineus* in the same number as those of the cercaria and that species does have a metacercarial stage in fish. Furthermore, the apparent retention of the cephalic glands in the young adult of *A. amiuri* may serve yet another purpose, viz., the penetration of the host's tissues by the young worm. Nor does the elimination of the second intermediate host seem likely in view of the observation of Van Cleave and Mueller (1934) that young and apparently recently excysted worms occur in the intestine of the bullhead. The discovery of cyst-like forms in the liver of *Schilbeodes gyrinus* by Pearse (1924) further suggests that the usual type of life cycle occurs in this species.

It seems unlikely that the young worm reaches the ovary by migrating from the anus to the urinogenital opening, and then up the oviducts. Many fish have been carefully examined in this connection and it would be expected that at least a few young worms would be found in the oviduct were this hazardous route the one which the parasite utilizes.

In view of the findings thus far, the most likely method of infection would seem to be ingestion of the metacarcariae, their excystment, penetration of the host intestine, and migration either through the body cavity or by way of the blood stream to the ovary where the worms develop to maturity. Of these routes the body cavity would seem more likely because adult worms have not been found elsewhere than in the ovary and occasionally the swim bladder, organs which because of their juxtaposition to the intestine would be the first encountered by the migrating forms. There is the added difficulty of the blood

stream imposed by the size of the worms, and the improbability of their being able to pass through the capillary networks intervening between the portal circulation of the host and the arterial blood supply of its ovaries. It is, of course, possible that the worms may migrate against the blood stream and thus reach the gonads without the necessity of passing through the capillary systems of the portal circulation and gills.

There is strong evidence that the adult of *A. amiuri*, unlike trematodes living in the intestine, does not begin to discharge eggs soon after maturity is attained. Observations on host-parasite relationship reported below support this view, but the most spectacular evidence is the behavior of the worms when removed from the host and placed in water (figs. 39 to 45). They immediately begin a slow steady contraction of the ventral muscles (fig. 40) so that the dorsal surface of the body becomes convex and the ventral concave. As this continues and the worm bends until the ends may meet (fig. 41), the uterus shortens until it is localized in the middle of the body, causing a prominent bulge on the dorsal surface of the worm. With continued contraction, the uterus ruptures through the body wall (figs. 42 and 43), which rolls back. Then the wall of the uterus bursts, projecting a stream of eggs several millimeters into the water. Only a few eggs remain in the body of the parasite (figs. 44 and 45). Worms placed in saline and left undistrubed do not discharge their eggs in this manner and will remain alive in the refrigerator for several days. On transfer to water, however, they respond as described. The process requires from 30 to 60 seconds. In view of these observations it is believed that the parasites are eliminated from the host at the time of spawning and that their eggs are dispersed in the manner described.

Vogel (1934) was successful in obtaining the infection of snails in the laboratory by feeding them large numbers of eggs of *Opisthorchis felineus*. This was tried in the case of *A. amiuri* but was not successful. Both young and mature snails of the genera *Pleurocera, Goniobasis* and *Campeloma,* as well as two pulmonate species were fed eggs containing active miracidia and their feces examined during a period of 24 hours. In all cases large numbers of intact eggs were recovered in the fecal masses, and in some instances apparently empty shells were observed. On one occasion an extremely active miracidium was found in the feces of a small *Goniobasis livescens*. After several minutes, the operculum of the egg opened and the miracidium was released. It moved rather swiftly for about 30 seconds and then disintegrated. The exposed snails were maintained in the laboratory for several weeks and periodically specimens were crushed and examined for larval forms with negative results.

HOST-PARASITE RELATIONSHIP IN THE DEFINITIVE HOST

Acetodextra amiuri apparently does not possess a very high degree of host specificity, since it is known to occur in three species of catfish, several species of bullheads and the miller's thumb. On the other hand, the trematode shows a strong preference for the female catfish, at least of species of *Ictalurus*. Of the 20 females examined in this study, 16 (80%) were found to harbor the parasite, while of the males only 3 of 22 (14%) were positive with one or two moribund or degenerate worms in the swim bladder. There never was any evidence of parasites in the testes of male catfish. It should be mentioned that

two of the four females which were negative for *A. amiuri* were immature.

In describing *A. amiuri* from the swim bladder of the host, Stafford (1900) and Pearse (1924) stated that the worms were inactive. This was true of specimens recovered in the present study from that site, the worm being greyish in color and moribund or degenerate. In one case of extreme infection of the ovary, worms also showed no sign of activity; nevertheless, when placed in tap water, they extruded their eggs in the manner described above for active specimens. They had apparently run the extreme course of development in the definitive host and had become inactive as the uterus attained maximum distension with eggs. In other cases of ovarian infection, the worms were very motile and in good condition.

In heavy infections, there frequently were found scattered throughout the ovary of the fish, several masses of *A. amiuri* eggs encapsulated in fibrous tissue. These masses varied considerably in size and the shape ranged from a spherical to an extremely irregular one. Their origin is not clear, but their microscopic structure indicates that they are at least in part of host origin. Each consists of a mass of eggs interspersed with loose strands enmeshing what appears to be small, darkly staining, pyknotic nuclei. Whether the source of this matrix is worm tissue is difficult to say because of its poorly organized nature. However, the surface of the mass consists of tissue that seems to be of host origin. This region contains cells which have well defined nuclei and could be identified as macrophages and fibroblasts. Among these cellular elements are hyaline layers which are very irregular in contour and can be traced for considerable distances. This membrane is identical in thickness and staining properties to the vitelline membrane of the egg. If eggs are the source of the membrane, a large number of the host's eggs must have been destroyed to account for the amount of such material found in the cysts. There are two possible explanations of these masses: (1) worms, after reaching full maturity, may die and a cellular reaction on the part of the host then lay down the tissue described, thus enclosing the body of the worm which then degenerates; or (2) worms may extrude eggs which collect in masses and are then enclosed in tissue of host origin. It cannot be said which of these explanations is the correct one. There is no evidence whatever that the mature worms liberate eggs more or less continuously from the uterus as is ordinarily the case in other species of trematodes. On the contrary, numerous sections of heavily infected ovaries have never been found to contain free eggs of the parasite. Thus it seems unlikely that the masses described above are formed by a host reaction to eggs liberated in the ovary. On the other hand, traces of tissue within the masses may well be of parasite origin. If this is true, the large size of many such masses and the number of eggs within them, indicates that more than one worm may contribute to the formation of a single mass. In addition to these large masses, there are sometimes observed smaller dark bodies consisting mostly if not entirely of eggs. These may represent earlier stages in the formation of the larger masses.

Several observations suggest that the formation of egg masses is an atypical phenomenon due primarily to the parasites being retained in the ovary of the host longer than necessary for them to become fully gravid. Observations described above suggest that worms and their eggs escape when the fish spawns

and that this is the typical manner in which the life cycle of the parasite is continued. Although the time required for the trematode to become gravid after reaching the ovary of the host is unknown, it is conceivable that the fish may become infected well before it reaches maturity, thus increasing the time that the parasite must remain in the ovary well beyond that which it would be required to remain in older fish. Under such conditions, the worm might become mature and, lacking the opportunity to escape in the normal manner, i.e., with the eggs of the host, might die and form the matrix of the masses described.

Although very young worms predominate among parasites observed in the ovaries of the fish after spawning, there are many that contain eggs. Whether or not such older worms failed to escape when the fish spawned or for some reason developed more rapidly than others is not known. It seems likely that at least a few worms, some more or less mature, may be retained in the ovary since cases have been observed in which a few mature eggs of the fish had not been discharged at spawning time. Such eggs evidently are resorbed and it is possible that this process might have an adverse effect on the parasites. Even if this is not the case, such worms would be required to remain in the ovary long after they become fully gravid. Before there is an opportunity to escape, then, the worms may die and degenerate, accounting for the formation of the egg masses.

As many as 1078 adults of *A. amiuri* were counted in a single ovary of *Ictalurus punctatus*. Such massive infections are common and they, as well as the histozoic or even cytozoic habits of the parasites, imply more severe damage to the host than may be caused by coelozoic trematodes.

There is no question that this species destroys ovarian tissue and eggs. On several occasions very young worms have been found within the developing eggs of the host (fig. 38). This situation as first observed in sections and seen later in fresh material in which the worms were very active, writhing and twisting within the egg almost constantly. Severe mechanical injury if no other must result from this activity of the parasite. In sections, eggs containing young worms are altered in appearance, lacking the homogeneous yolk characteristic of normal eggs of the same size. In fresh material, the infected egg follicle appears wrinkled and the egg is paler yellow in color than is normal. There is no doubt that the worm consumes yolk: the intestine is filled with it, even in the large mature worm which occurs free in the ovary and approaches the egg in volume. It thus seems likely that each parasite may destroy several eggs as it grows to maturity. Consequently, the host would seem to suffer a loss of considerable number of eggs in cases of massive infection. If this is true, there may be a compensatory activity of the germinal epithelium because in the cases of heaviest infections observed which were shortly before spawning time, the ovary was filled with well formed eggs. Many of these, however, contained very young worms and for that reason probably would not develop.

SUMMARY

The biology of *Acetodextra amiuri* in the definitive host and the morphology of the adult worm and miracidium are described. The symmetry of the miracidium is held to be an invalid distinction between the Opisthorchiidae and

the Heterophyidae. It is shown that the ovary of the catfish and not the swim bladder is the principal site of infection and evidence is presented to the effect that the entire worm is cast out of the host when it spawns instead of the parasite's eggs being voided in the usual manner.

In redescribing the adult, the excretory system and gametogenesis are included. The flame cell formula is 2[(4+4+4)+(4+4+4)] and the diploid chromosome number is twelve. It was determined that in spermatogenesis, the cytoplasm as well as the nucleus contributes to the formation of the sperm.

REFERENCES

ANDERSON, M. G. 1935—Gametogenesis in the primary generation of a digenetic trematode, *Proterometra macrostoma*. Trans. Amer. Micros. Soc. 54:271-297.

ARNOLD, J. G. 1934—Some trematodes of the common bullhead *Ameiurus nebulosus* (Le Sueur). Ibid. 53:267-276.

BAER, J. G. 1943—Les trématodes parasites de la musaraigne d'eau *Neomys fodiens* (Schreb.). Bull. Soc. Neuchatel. Sci. Nat. 68:33-84.

BANGHAM, R. V. AND G. W. HUNTER 1939—Studies of fish parasites of Lake Erie: Distribution studies. Zoologica 24:385-448.

BURNS, W. C. AND I. PRATT 1953—The life cycle of *Metagonimoides oregonensis* Price (Trematoda: Heterophyidae). J. Parasit. 29:60-69.

BUTTNER, A. 1951—La progénèse chez les trématodes digénétiques (suite). Recherches personelles sur deux espèces progénétiques déjà connues: *Ratzia joyeuxi* (E. Brumpt, 1922) et *Pleurogenes medians* (Olsson, 1876). Ann. Parasit. 26:138-189.

——— 1952—Nouvelle démonstration d'un cycle abrégé chez *Ratzia joyeuxi* (Trematoda: Opisthorchiidae). Compt. Rend. Acad. Sci. Paris 234:673-675.

CABLE, R. M. 1931—Studies on the germ cell cycle of *Cryptocotyle lingua* Creplin. I. Gametogenesis in the adult. Quart. J. Micros. Sci. 74:563-589.

——— 1952—Studies on marine digenetic trematodes of Puerto Rico. Four species of magnacercous heterophyid cercariae with zygocercous aggregation in one. J. Parasit. 38 (4, sec. 2):28.

——— AND A. V. HUNNINEN 1942—Studies on the life history of *Siphodera vinaledwardsii* (Linton) (Trematoda: Cryptogonimidae). Ibid. 28:407-422.

CHEN, P. D. 1937—The germ cell cycle in the trematode, *Paragonimus kellicotti* Ward. Trans. Amer. Micros. Soc. 56:208-236.

CIUREA, I. 1933—Les vers parasites de l'homme, des mammifères, et des oiseaux provenant des poissons du Danube et de la Mer Noire. Premier mémoire. Trématodes, famille Heterophyidae Odhner. Arch. Roumaines Path. Exp. Microbiol. 6:5-134.

DINGLER, M. 1910—Über die Spermatogenese des *Dicrocoelium lanceatum* Stil. et Hass. Arch. f. Zellforsch. 4:672-712.

FAUST, E. C. 1929—Human Helminthology. Philadelphia.

——— O. K. KHAW, K. E. YAO AND Y. A. CHAO 1927—Studies on *Clonorchis sinensis* (Cobbold) Amer. J. Hyg. Monogr. Ser. 8:1-284.

GILLE, O. K. 1914—Untersuchungen über die Eireifung, Befruchtung und Zellteilung von *Gyrodactylus elegans* v. Nordmann. Arch. f. Zellforsch. 12:415-456.

GOLDSCHMIDT, R. 1908—Ueber das Verhalten des Chromatins bei der Eireifung und Befruchtung des *Dicrocoelium lanceatum* Sti. et Hass. (*Distomum lanceolatum*). Ibid. 1:232-244.

HUNTER, G. W. AND W. S. HUNTER 1932—X. Studies on parasites of fish and fish-eating birds. Biol. Sur. VI. Oswegatchie and Black River systems. 1931 suppl. 21st Ann. Rep. N. Y. State Cons. Dept. :252-271.

KATHARINER, L. 1904—Ueber die Entwicklung von *Gyrodactylus elegans* v. Nordm. Zool. Jahrb. Suppl. 7:519-550.

KOMIYA, Y. AND T. TAJIMI 1940—Study of *Clonorchis sinensis* in the district of Shanghai. 6. The life cycle of *Exorchis oviformis*, with special reference of the similarity of its larval forms to that of *Clonorchis sinensis*. J. Shanghai Sci. Inst. Sec. 4:109-123.

MARTIN, W. E. 1950a—*Phocitremoides ovale* n. gen., n. sp. (Trematoda: Opisthorchiidae), with observations on its life cycle. J. Parasit. 36:552-558.

——— 1950b—*Euhaplorchis californiensis* n. g., n. sp., Heterophyidae, Trematoda, with notes on its life cycle. Trans. Amer. Micros. Soc. 69:194-209.

——— 1950c—*Parastictodora hancocki* n. gen., n. sp. (Trematoda: Heterophyidae), with observations on its life cycle. J. Parasit. 36:360-370.

——— 1951—*Pygidiopsoides spindalis* n. gen., n. sp., (Heterophyidae: Trematoda) and its second intermediate host. Ibid. 37:297-300.

MUELLER, J. F. 1934—Parasites of Oneida Lake fishes. Part 4. Additional notes on parasites of Oneida Lake fishes including descriptions of new species. Roosevelt Wild Life Ann. 3:335-373.

——— AND H. J. VAN CLEAVE 1932—Parasites of Oneida Lake fishes. Part 2. Descriptions of new species and some general taxonomic considerations, especially concerning the trematode family Heterophyidae. Ibid. 3:79-137.

PEARSE, A. S. 1924—Observations on parasitic worms from Wisconsin fishes. Trans. Wis. Acad. Sci. 21:147-160.

PRICE, E. W. 1940—A review of the trematode superfamily Opisthorchioidea. Proc. Helm. Soc. Washington 7:1-13.

SILLMAN, E. I. 1953—Notes on the life history of *Opisthorchis tonkae* Wallace and Penner, 1939 (Trematoda: Opisthorchiidae) J. Parasit. 39(4, sec. 2):21.

STAFFORD, J. 1900—Some undescribed trematodes. Zool. Jahrb. Abt. Syst. 13:399-414.

STUNKARD, H. W. 1930—The life history of *Cryptocotyle lingua* (Creplin), with notes on the physiology of the metacercaria. J. Morph. Physiol. 50:143-191.

TAO, C. S. 1948—Notes on the study of life-cycle of *Metorchis orientalis* and *M. taiwanensis*. Chinese Rev. Trop. Med. 1:9-14.

VAN CLEAVE, H. J. AND J. F. MUELLER 1931—The systematic position of some trematodes from fresh-water fishes of North America. J. Parasit. 18:132-133.

——— AND ——— 1934—Parasites of Oneida Lake Fishes, Part 3. Roosevelt Wild Life Ann. 3:161-334.

VAN DER WOUDE, A. 1954—Germ cell cycle of *Megalodiscus temperatus* (Stafford, 1905) Harwood, 1932 (Paramphistomidae: Trematoda). Amer. Midl. Nat. 51:172-202.

VOGEL, H. 1934—Der Entwicklungszyklus von *Opisthorchis felineus* (Riv.) nebst Bemerkungen über die Systematik und Epidemiologie. Zoologica 86:1-103.

WILLEY, C. H. AND G. C. GODMAN 1941—Gametogenesis in the trematode *Zygocotyle lunata*. Anat. Rec. 81(suppl.):78.

——— AND S. KOULISH 1950—Development of germ cells in the adult stage of the digenetic trematode, *Gorgoderina attenuata* Stafford, 1902. J. Parasit. 36:67-75.

WITENBERG, G. 1929—Studies on the trematode family Heterophyidae. Ann. Trop. Med. Parasit. 23:131-239.

WOODHEAD, A. E. 1931—The germ cell cycle in the trematode family Bucephalidae. Trans. Amer. Micros. Soc. 50:169-188.

YAMAGUTI, S. 1938—Zur Entwicklungsgeschichte von *Centrocestus armatus* (Tanabe) mit besonderer Berüchsichtigung der cercarie. Ztschr. Parasitenk. 10:293-296.

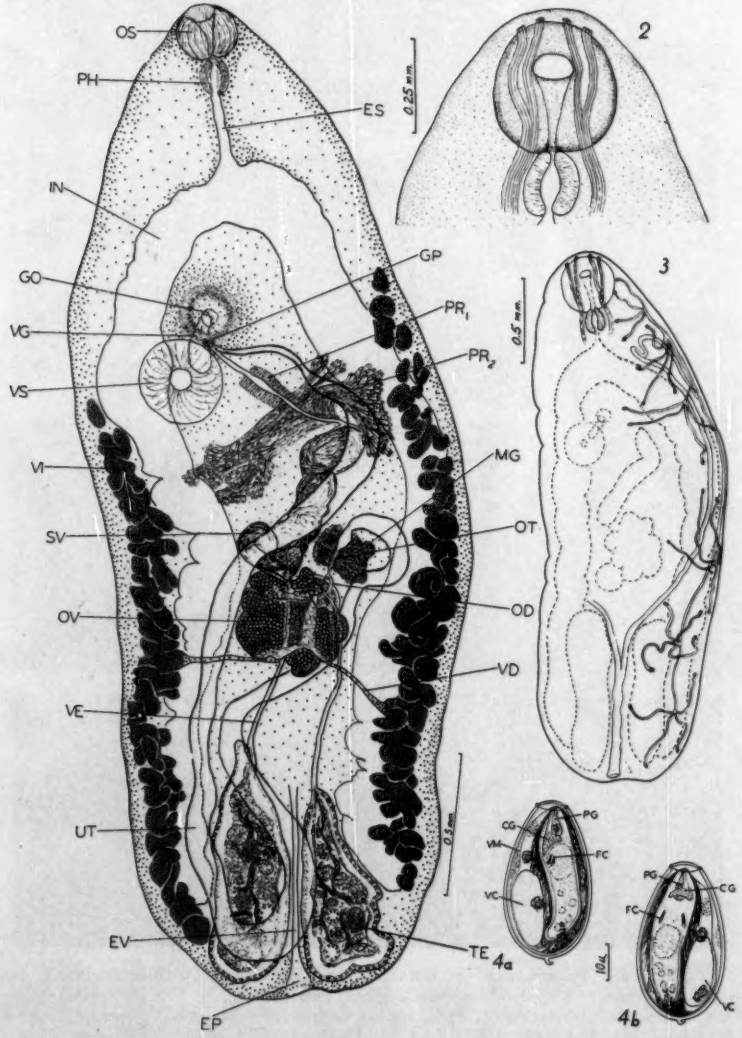
YOSUFZAI, H. K. 1952—Cytological studies on the spermatogenesis of *Fasciola hepatica* L. Cellule 55:7-19.

——— 1953—Cytological studies on the oogenesis of *Fasciola hepatica* L. Ibid. 55: 167-176.

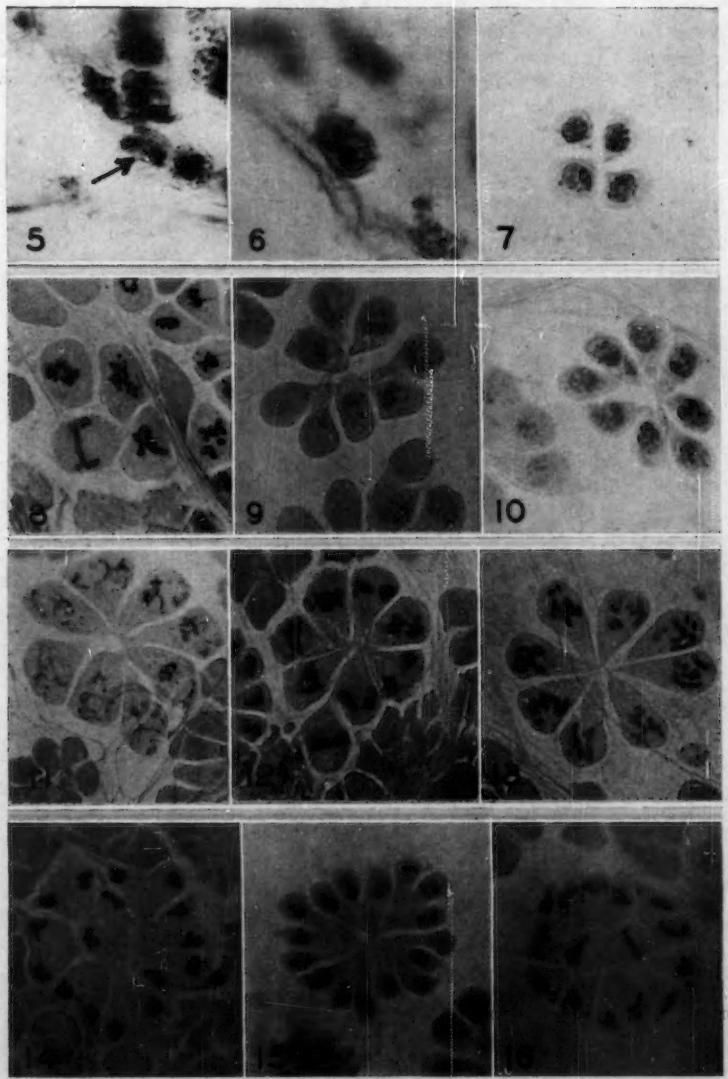
ABBREVIATIONS

CG—cephalic gland; EP—excretory pore; ES—esophagus; EV—excretory vesicle; FC—flame cell; GO—gonotyl; GP—genital pore; IN—intestine; MG—Mehlis' gland; OD—oviduct; OS—oral sucker; OT—oötype; OV—ovary; PB^1—first polar body; PG—primi-

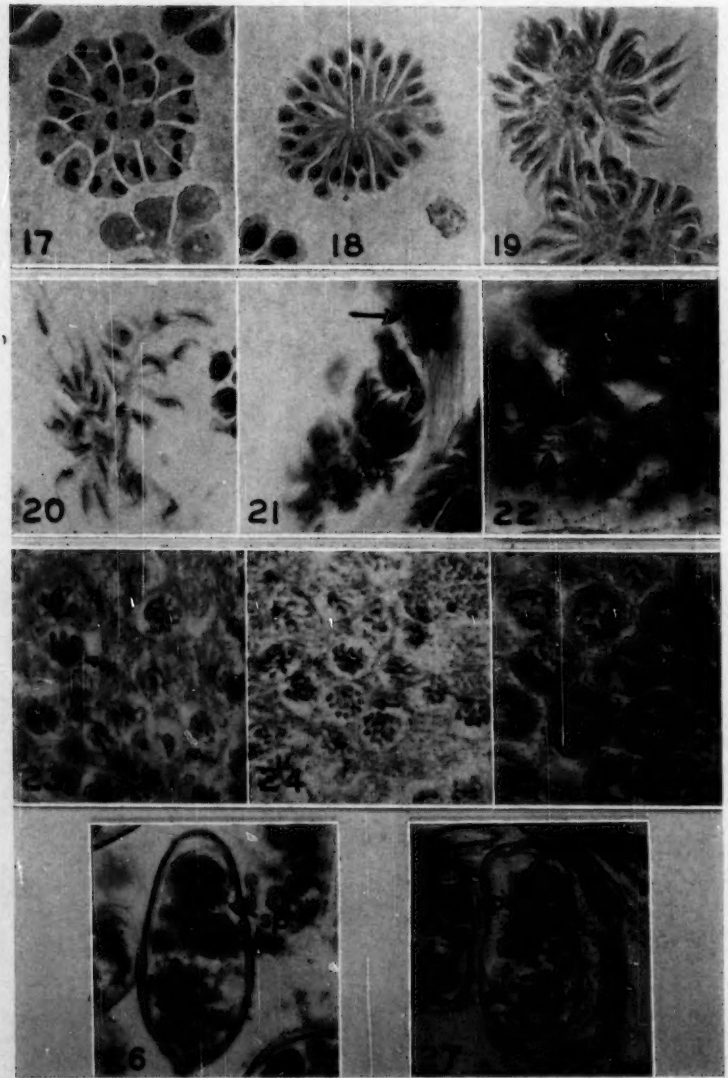
tive gut; PH—pharynx; PR_1—prostate, distal portion; PR_2—prostate, proximal portion; SP—sperm; SV—seminal vesicle; TE—testis; UT—uterus; VC—vacuole; VD—vitelline duct; VE—vas efferens; VG—ventrogenital pit; VI—vitellaria; VM—vitelline membrane; VS—ventral sucker.



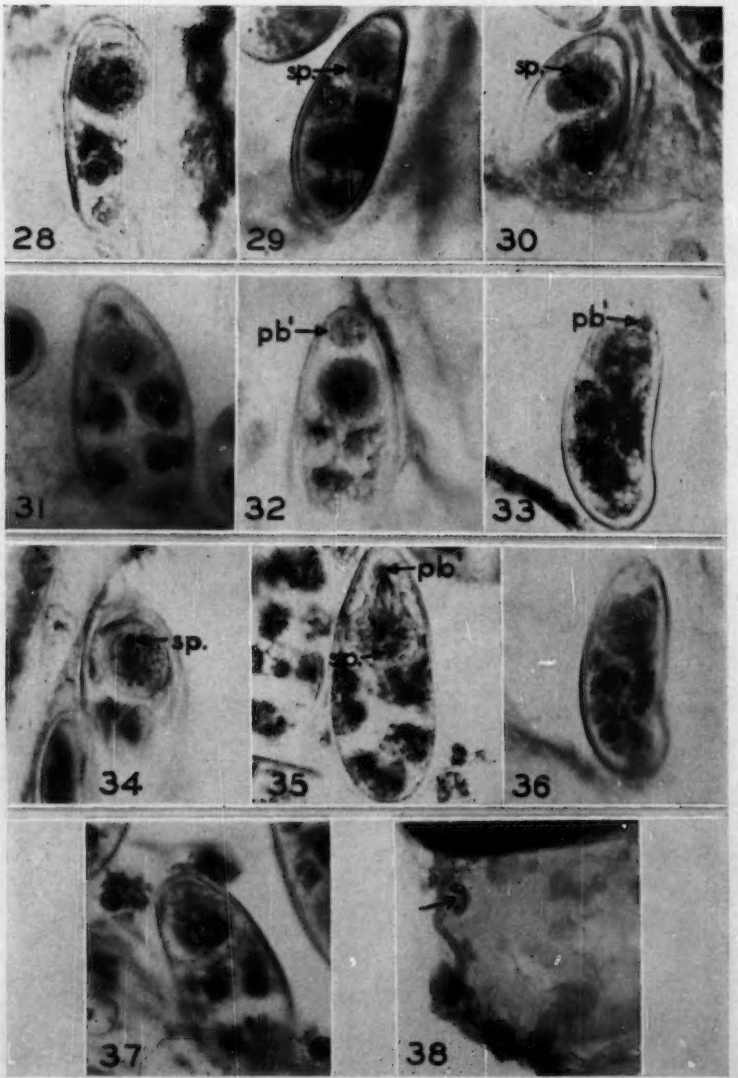
Figs 1-4.—*Acetodextra amiuri*. 1. Adult, ventral view; 2. Young adult, detail of cephalic gland ducts; 3. Excretory system of young adult; 4. Egg containing miracidium in (a) lateral and (b) frontal views.



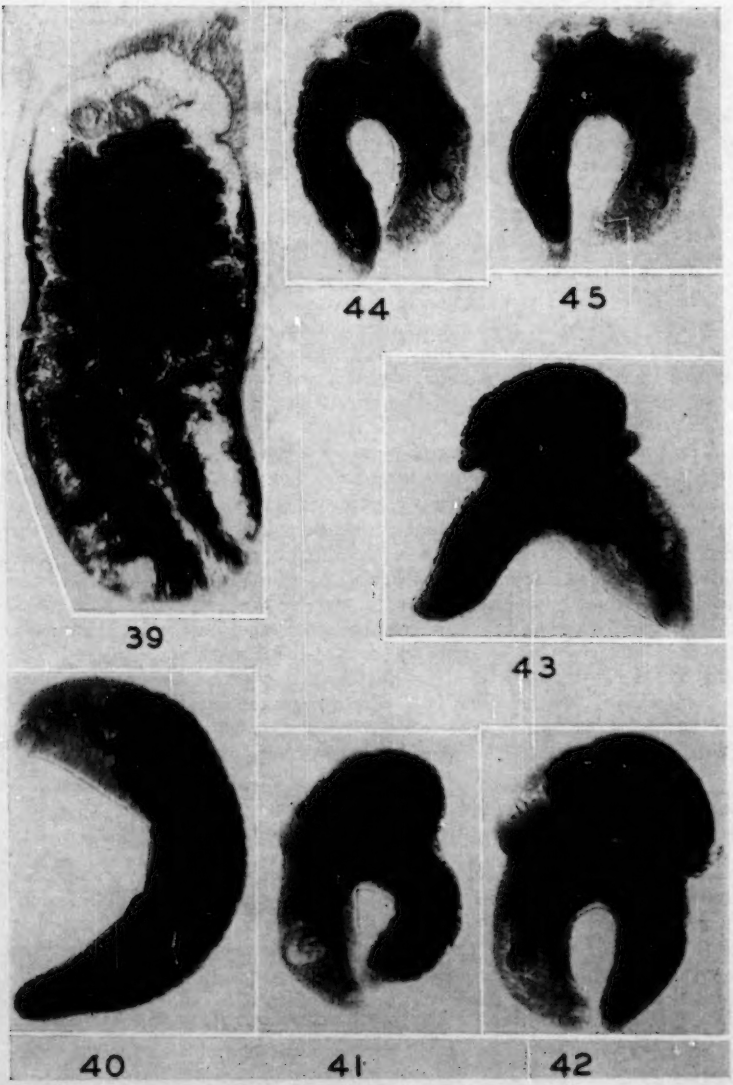
Figs. 5-16.—Gametogenesis in *Acetodextra amiuri*. 5. Primary spermatogonium, late anaphase (arrow); 6. Secondary spermatogonia, interphase. 7, 8. Tertiary spermatogonia. 7. Chromosomes condensing; 8. Chromosomes condensed. 9-14. Primary spermatocytes. 9. Interphase; 10. Chromatin condensing; 11. Further condensation; 12. Bivalent chromosomes; 13. Separation of bivalent chromosomes; 14. Near end of first maturation division. 15, 16. Secondary spermatocytes. 15. Interphase; 16. Chromosomes condensed for second maturation division. (All photomicrographs at 1600 diameters)



Figs. 17-27.—Gametogenesis in *Acetodextra amiuri*. 17. Secondary spermatocytes, second maturation division; 18. Spermatids with rounded nuclei; 19. Elongating spermatids; 20. Further elongation of spermatids to become sperms; 21. Spermatozoa (arrow); 22. Oögonia, interphase and anaphase (arrow). 23-25. Primary oöcytes. 23. "Bouquet" stage; 24. Cross section of "bouquet" (arrow); 25. Near oöcapt. 26, 27. Newly formed egg. 26. Showing primary oöcyte and sperm (arrow) in cross section; 27. With sperm over surface of primary oöcyte. (All photomicrographs at 1600 diameters).



Figs. 28-38.—Gametogenesis in *Acetodextra amiuri*. 28. Egg with primary oöcyte showing condensation of chromosomes before first maturation division; 29. Egg showing bivalent chromosomes of first maturation division of oöcyte; 30. Side view of stage shown in fig. 29; 31. Late anaphase of first maturation division of oöcyte; 32, 33. Secondary oöcyte. 32. Vesicular first polar body; 33. Condensed first polar body. 34, 35. Second maturation division. 34. Oöcyte; 35. Oöcyte just before second polar body is formed. 36. Male and female pronuclei; 37, Fertilization, pronuclei fusing; 38. Young *Acetodextra amiuri* (arrow) within egg of host. (Photomicrographs except fig. 38 at 1600 diameters)



Figs. 39-45.—39. Gravid adult of *Acetodextra amiuri* showing extent of uterus before process of egg extrusion begins. 40-45. Successive phases of egg extrusion. 40. The worm first flexes ventrally; 41, 42. The uterus shortens and forms a dorsal bulge; 43. Ruptures through the body wall; 44, 45. Finally bursts.

North American Freshwater Tetraonchinae

John D. Mizelle and Paul S. Stokely
University of Notre Dame, Notre Dame, Indiana

Benjamin J. Jaskoski
Loyola University, Chicago, Illinois

Aaron P. Seamster and Lawrence H. Monaco
Del Mar College, Corpus Christi, Texas

The subfamily Tetraonchinae is composed of twenty recognized genera (Sproston 1946). North American investigations on this group began in 1932 when Van Cleave and Mueller described *Urocleidus aculeatus*. Presently there are four North American freshwater genera and two exotic genera that have freshwater representatives on this continent. An additional genus was proposed by Mizelle (1955) and is defined herein.

The present paper was planned to aid workers in this particular area of parasitology and to stimulate others to participate in research on the Monogenea. The host-list section enables an investigator to know the possibilities regarding the identity of a species after the host has been identified. Reference to the genera-and-species section will provide information concerning papers 1) containing original descriptions, 2) synonymy, and 3) the hosts and localities from which given species have been recorded together with the authors involved. In cases where a species has been cited from the same host and locality more than once by a given author, only the date of the first citation is given. The Reelfoot Lake locality has been changed in all cases from Ridgely, Tennessee to Tiptonville, Tennessee. This in no way changes the type locality in the case of new species but merely cites a more appropriate village near the lake as advised by Dr. C. L. Baker of Southwestern College at Memphis.

Genera and Species

Anchoradiscus Mizelle, 1941

Diagnosis—Tetraonchinae with bases of the two pairs of anchors situated parallel to, and developed to extend through the greater portion of a frontal plane of, the discoidal haptor. Anchor shafts vestigial or wanting; anchor points (recurved) directed laterally. Haptoral bars two, attached to the ventral (lateral) surfaces of the anchor bases and articulated with each other in midportions. Each of the seven pairs of hooks situated on the haptoral margin and differentiated into a base, a slender solid shaft, a sickle-shaped termination, and an opposable piece. Copulatory complex consisting of a cirrus and accessory piece; vagina sinistral. Two pairs of eye spots; members of posterior pair larger than those of anterior pair. Parasitic on gills of freshwater fishes.

Type species—*Anchoradiscus anchoradiscus* Mizelle, 1941.

A. anchoradiscus Mizelle, 1941.—*Lepomis microlophus* (Günther), Englewood Ditch, Englewood, Fla.; Myakka River, State Park, East Sarasota,

Fla., Lake Okeechobee, Moore Haven, Fla., Everglades Canal, Naples, Fla. (Mizelle 1941). *Lepomis macrochirus* Rafinesque, Canal, North Everglades, Fla. (Mizelle 1941).

A. TRIANGULARIS (Summers, 1937) Mizelle, 1941. (Syn. *Actinocleidus triangularis* Summers, 1937).—*Lepomis symmetricus* Forbes, Freshwater Lakes and Bayous near Baton Rouge, La. (Summers 1937); Baton Rouge, La. (Summers & Bennett 1938).

ACTINOCLEIDUS Mueller, 1937

Diagnosis—Tetraonchinae with trunk, eyes, gut, gonads, cirrus, accessory piece, vagina (when present), and vitellaria as in *Cleidodiscus*. Haptor distinct and discoidal; armed with two pairs of anchors and seven pairs of hooks. Anchors ventral, approximately uniform in size and shape, bases of each pair connected by a transverse bar; bars articulate with each other. Parasitic on gills of freshwater fishes.

Type species.—*Actinocleidus oculatus* (Mueller, 1934) Mueller, 1937.

A. ARTICULARIS (Mizelle, 1936) Mueller, 1937. (Syn. *Cleidodiscus articularis* Mizelle, 1936).—*Lepomis megalotis* (Rafinesque), Embarrass River, Urbana, Ill. (Mizelle 1936); Cove Creek, Caryville, Tenn. (Mizelle 1940).

A. BAKERI Mizelle & Cronin, 1943.—*Lepomis microlophus* (Günther), Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943).

A. BIFIDUS Mizelle & Cronin, 1943.—*Lepomis microlophus* (Günther), Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943).

A. BREVICIRRUS Mizelle & Jaskoksi, 1942.—*Lepomis miniatus* Jordan, Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Jaskoski 1942).

A. CRESCENTIS Mizelle & Cronin, 1943.—*Lepomis microlophus* (Günther), Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943).

A. FERGUSONI Mizelle, 1938.—*Lepomis macrochirus* Rafinesque, Lake Senachwine, Henry, Ill.; Boomer Creek, Stillwater, Okla. (Mizelle 1938a); Local Ponds and Streams near Stillwater, Okla. (Seamster 1938); Reelfoot Lake, Tiptonville, Tenn., Lake Okeechobee, Moore Haven, Fla., Canal, North Everglades, Fla. (Mizelle & Brennan 1942); Bass Lake (Hatchery), Carrol Lake, Madeline Lake, Minocqua Thoroughfare along Woodruff Hatchery (all) near Woodruff, Wis., Yellow River Flowage next to Fisheries Laboratory near Spooner, Wis. (Mizelle & Regensberger 1945); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b). *Chaenobryttus coronarius* (Bartram), Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b). *Lepomis humilis* (Girard), Local Ponds and Streams near Stillwater, Okla. (Seamster 1938).

A. FLAGELLATUS Mizelle & Seamster, 1939.[1]—*Chaenobryttus coronarius* (Bartram) Roadside Canal, Naples, Fla., Roadside Ditch, Englewood, Fla. (Mizelle & Seamster 1939); Reelfoot Lake, Tiptonville, Tenn. (Mizelle &

[1] The report of *A. flagellatus* from *L. macrochirus* by Hargis (1952b) was admitted to be erroneous (Hargis 1953).

Cronin 1943); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b).

A. FUSIFORMIS (Mueller, 1934) Mueller, 1937 (Syn. *Ancyrocephalus cruciatus* Wedl, 1858, see Cooper, 1915; *Cleidodiscus fusiformis* Mueller, 1934). —*Micropterus dolomieu* Lacépède, State Fish Hatchery Reservoir, Constantia, N. Y. (Mueller 1934); Ohio Hatcheries, London, Ohio, Syracuse, N. Y. (Mueller 1936); Cove Creek, Caryville, Tenn. (Mizelle 1940). *Micropterus punctulatus* (Rafinesque), Norris Lake, Norris, Tenn., Cold Creek below Norris Dam (Tenn.), Cove Creek, Caryville, Tenn. (Mizelle 1940). *Micropterus salmoides* (Lacépède), Peace River, Fla. (Mueller 1937); Local Ponds and Streams near Stillwater, Okla. (Seamster 1938); New Roads, La. (Summers & Bennett 1938); Hatchery, Norris, Tenn. (Mizelle 1940); Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943); Pinkeye Lake near Land O'Lakes, Wis., Chetac Lake near Birchwood, Wis. (Mizelle & Regensberger 1945). Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b).

A. GIBBOSUS Mizelle & Donahue, 1944.—*Lepomis gibbosus* (Linnaeus), Opeongo Lake in Algonquin Park, Ontario, Canada (Mizelle & Donahue 1944).

A. GRACILIS Mueller, 1937.—*Lepomis macrochirus* Rafinesque, Fla. (Mueller 1937).

A. HARQUEBUS Mizelle & Cronin, 1943.—*Lepomis microlophus* (Günther), Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943).

A. INCUS Mizelle & Donahue, 1944.—*Lepomis gibbosus* (Linnaeus), Opeongo Lake in Algonquin Park, Ontario, Canada (Mizelle & Donahue 1944).

A. LONGUS Mizelle, 1938.—*Lepomis cyanellus* Rafinesque, Embarrass River, Urbana, Ill. (Mizelle 1938); Boomer Creek, Stillwater, Okla. (Mizelle 1938a); Local Ponds and Streams near Stillwater, Okla. (Seamster 1938); Urbana, Ill. (Kimpel 1939). *Lepomis macrochirus* Rafinesque, Baton Rouge, La. (Summers & Bennett 1938).

A. MACULATUS Mueller, 1937.—*Lepomis gibbosus* (Linnaeus), Fla. (Mueller 1937). *Lepomis microlophus* (Günther), Myakka River, State Park, East Sarasota, Fla., Everglades Canal, Naples, Fla. (Mizelle 1941a).

A. OCULATUS (Mueller, 1934) Mueller, 1937. (Syn. *Cleidodiscus oculatus Mueller*, 1934).—*Lepomis gibbosus* (Linnaeus), State Fish Hatchery Reservoir, Constantia, N. Y. (Mueller 1934); Syracuse, N. Y. (Mueller 1936); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b). "Sunfish," Cross Lake, N. Y. (Mueller 1936); Long and Opeongo lakes in Algonquin Park, Ontario, Canada (Mizelle & Donahue 1944). *Lepomis macrochirus* Rafinesque, Baton Rouge, La. (Summers & Bennett 1938).

A. OKEECHOBEENSIS Mizelle & Seamster, 1939.—*Chaenobryttus coronarius* (Bartram), Lake Okeechobee, Moore Haven, Fla. (Mizelle & Seamster 1939); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b).

A. RECURVATUS Mizelle & Donahue, 1944.—*Lepomis gibbosus* (Linnaeus), Costello, Long, Opeongo, and Proulx lakes, (all) Algonquin Park, Ontario,

Canada (Mizelle & Donahue 1944); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b).

A. SCAPULARIS Mizelle & Donahue, 1944.—*Lepomis gibbosus* (Linnaeus), Opeongo Lake in Algonquin Park, Ontario, Canada (Mizelle & Donahue 1944).

A. SIGMOIDEUS Mizelle & Donahue 1944.—*Lepomis gibbosus* (Linnaeus), Costello, Long, Opeongo, and Proulx lakes, (all) Algonquin Park, Ontario, Canada (Mizelle & Donahue 1944); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b).

A. SUBTRIANGULARIS Mizelle & Jaskoski, 1942.—*Lepomis miniatus* Jordan, Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Jaskoski 1942).

Clavunculus, new genus

Diagnosis—Tetraonchinae with trunk, eyes, gut, gonads, cirrus, accessory piece, vagina (when present), and vitellaria as in *Cleidodiscus*. Haptor distinct, umbrella-like with scalloped margin, and provided with two pairs of anchors situated on small protuberance in center of ventral surface. Bases of each pair of anchors connected by a bar; bars articulate with each other. Seven pairs of haptoral hooks; each marginal indentation of haptor usually provided with one hook. Parasitic on the gills of freshwater fishes.

Type species—*Clavunculus bursatus* (Mueller, 1936).

C. BIFURCATUS (Mizelle, 1941) (Syn. *Actinocleidus bifurcatus* Mizelle, 1941).—*Lepomis microlophus* (Günther), Everglades Canal, Naples, Fla., Lake Okeechobee, Moore Haven, Fla. (Mizelle 1941a).

C. BURSATUS (Mueller, 1936) (Syn. *Ancyrocephalus bursatus* Mueller, 1936; *Actinocleidus bursatus* (Mueller, 1936) Mueller, 1937).—*Micropterus salmoides* (Lacépède), London, Ohio (Mueller 1936); Peace River, Fla. (Mueller 1937). *Micropterus dolomieu* Lacépède, and *M. punctulatus* (Rafinesque), Cove Creek, Caryville, Tenn. (Mizelle 1940). *Lepomis macrochirus* Rafinesque, Lake Okeechobee, Moore Haven, Fla. (Mizelle & Brennan 1942).

C. UNGUIS (Mizelle & Cronin, 1943) (Syn. *Actinocleidus unguis* Mizelle & Cronin, 1943).—*Micropterus salmoides* (Lacépède), Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943); Pinkeye Lake near Land O'Lakes, Wis. (Mizelle & Regensberger 1945); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b).

CLEIDODISCUS Mueller, 1934

Synonyms—*Leptocleidus* Mueller, 1936, in part; *Tetracleidus* Mueller, 1936 in part (See Mizelle and Hughes 1938).

Diagnosis—Tetraonchinae somewhat flattened dorsoventrally and with trunk narrowly elliptical in outline (dorsal view). Eyes four, one pair larger than, and posterior to, the other. Gut bifurcate, without diverticula; rami confluent posteriorly. Gonads near middle of body. Cirrus usually a simple cuticu-

larized tube. Accessory piece always present and generally articulated basally with the cirrus. Vagina usually present and opening on left[2] margin near midlength of trunk. Vitellaria consisting of numerous, small, discrete follicles arranged in a pair of lateral bands extending from the pharyngeal region to, or into, the peduncle; the bands always posteriorly, and sometimes anteriorly, confluent. Haptor generally distinct, discoidal or subhexagonal; armed with 2 pairs of anchors and seven pairs of hooks. Anchors, one pair dorsal and the other pair ventral, with superficial roots of each pair connected by a transverse bar; bars nonarticulate with each other. Parasitic on the gills of freshwater fishes.

Type species—*Cleidodiscus robustus* Mueller, 1934.

C. ACULEATUS (Van Cleave & Mueller, 1932) Mizelle & Regensberger, 1945. (Syn. *Ancyrocephalus aculeatus* Van Cleave & Mueller, 1932; *Urocleidus aculeatus* (Van Cleave & Mueller, 1932) Mueller, 1934).—*Stizostedion vitreum* (Mitchill), Oneida Lake, N. Y. (Van Cleave & Mueller 1932; Mueller, 1934). Clear Lake, Big Arbor Vitae Lake, Johnson Lake (all) near Woodruff, Wis., Squaw Lake near Lac Du Flambeau, Wis. (Mizelle & Regensberger 1945).

C. ALATUS Mueller, 1938.—*Ambloplites rupestris* (Rafinesque), Chautauqua Lake, N. Y. (Mueller 1938); Yellow River Flowage next to Fisheries Laboratory near Spooner, Wis., Blue Lake near Minocqua, Wis. (Mizelle & Regensberger 1945).

C. BANGHAMI (Mueller, 1936) Mizelle 1940. (Syn. *Tetracleidus banghami* Mueller, 1936; *Urocleidus banghami* (Mueller, 1936) Mizelle & Hughes, 1938).—*Micropterus dolomieu* Lacépède, London, Ohio (Mueller 1936); Cove Creek, Caryville, Tenn. (Mizelle 1940); Opeongo Lake in Algonquin Park, Ontario, Canada (Mizelle & Donahue 1944). *Micropterus punctulatus* (Rafinesque), Cove Creek, Caryville, Tenn. (Mizelle 1940).

C. BEDARDI Mizelle, 1936.—*Lepomis megalotis* (Rafinesque), Embarrass River, Urbana, Ill. (Mizelle 1936); Cove Creek, Caryville, Tenn. (Mizelle 1940).

C. BRACHUS Mueller, 1938.—*Semotilus atromaculatus* (Mitchill); French Creek near Panama, N. Y. (Mueller 1938); Fish Creek, Bayfield Co., Wis., Pine River, Clarence Co., Wis. (Mizelle & Klucka 1953). *Margariscus margarita* (Cope), French Creek near Panama, N. Y. (Mueller 1938).

C. CAPAX Mizelle, 1936.—*Pomoxis annularis* Rafinesque, Lake Decatur, Decatur, Ill., Illinois River, Havana, Ill. (Mizelle 1936); Reelfoot Lake, Tiptonville, Tenn., Miss. River in Ill. (Mizelle, La Grave, & O'Shaughnessy 1943). *Pomoxis nigro-maculatus* (LeSueur), Lake Senachwine, Henry, Ill., Illinois River, Havana, Ill. (Mizelle 1936); Lakeland, Md., Oneida Lake, N. Y. (Mueller 1937); Reelfoot Lake, Tiptonville, Tenn., Miss. River in Ill. (Mizelle, La Grave, & O'Shaughnessy 1943); Big Arbor Vitae Lake near Woodruff, Wis., Chetac Lake near Birchwood, Wis., Lake-du-Bay (Knowlton Flowage) near Mosinee, Wis. (Mizelle & Regensberger 1945); Swamp Pools

[2] The vagina is dextral in *C. banghami* (See Mizelle 1940).

and Bayous near Monroe, La. (Seamster 1948); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b).

C. CHELATUS Mizelle & Jaskoski, 1942.—*Lepomis miniatus* Jordan, Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Jaskoski 1942).

C. DIVERSUS Mizelle, 1938.—*Lepomis cyanellus* Rafinesque, Embarrass River, Urbana, Ill. (Mizelle 1938); Boomer Creek, Stillwater, Okla. (Mizelle 1938a); Local Ponds and Streams near Stillwater, Okla. (Seamster 1938).

C. FLORIDANUS Mueller, 1936. (Syn. *Cleidodiscus mirabilis* Mueller, 1937, in part).—*Ictalurus lacustris punctatus* (Rafinesque), Myakka River, Fla., Lake Okeechobee, Fla. (Mueller 1936a); St. Croix River, Burnett Co., Upper Lake Pepin, and Miss. River (all) Wis. (Mizelle & Klucka 1953); Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943). *Ameiurus melas* (Rafinesque), Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943). *Ictalurus furcatus* (LeSueur), Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943). *Ictalurus l. lacustris* (Walbaum), St. Croix River, Burnett Co., Upper Lake Pepin, and Miss. River (all) Wis. (Mizelle & Klucka 1953); Upper Lake Pepin, Miss. River (both) Wis. (Mizelle & Webb 1953); *Pilodictis olivaris* (Rafinesque), Miss. River (Mueller 1937).

C. LONGUS Mizelle, 1936.—*Pomoxis annularis* Rafinesque, Lake Decatur, Decatur, Ill. (Mizelle 1936); Salt Lake Fork of Big Vermilion River south of Oakwood, Ill., Boomer Creek, Stillwater, Okla. (Mizelle 1938a); Local Ponds and Streams near Stillwater, Okla. (Seamster 1938); Reelfoot Lake, Tiptonville, Tenn., Miss. River in Ill. (Mizelle, La Grave, & O'Shaughnessy 1943).

C. MEGALONCHUS (Mueller, 1936) Mizelle & Hughes, 1938. (Syn. *Tetraonchus unguiculatus* Wagener, 1857 (See Cooper 1915); *Ancyrocephalus paradoxus* Creplin, 1839 (See Cooper 1915); *Leptocleidus megalonchus* Mueller, 1936).—*Micropterus dolomieu* Lacépède, Lake Station on Georgian Bay, Canada (Cooper 1915); London, Ohio (Mueller 1936). *Ambloplites rupestris* (Rafinesque) and *Lepomis gibbosus* (Linnaeus), Canada, (Stafford 1905).

C. NEMATOCIRRUS Mueller, 1937.—*Lepomis gibbosus* (Linnaeus), Fla. (Mueller 1937). *Lepomis macrochirus* (Rafinesque), Baton Rouge, La. (Summers & Bennett 1938). *Lepomis microlophus* (Günther), Englewood Pond, Englewood, Fla., Everglades Canal, Naples, Fla., and Lake Okeechobee, Moore Haven, Fla. (Mizelle 1941a). *Lepomis megalotis* (Rafinesque), Swamp Pools and Bayous near Tremont, La. (Seamster 1948).

C. PRICEI Mueller, 1936.—*Ictalurus lacustris punctatus* (Rafinesque), Myakka River, Fla., Lake Okeechobee, Fla. (Mueller 1936a); Local Ponds and Streams near Stillwater, Okla. (Seamster 1938); Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943). *Ameiurus melas* (Rafinesque), Local Ponds and Streams near Stillwater, Okla. (Seamster 1938); Baton Rouge, La. (Summers & Bennett 1938); Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943); Opeongo Lake in Algonquin Park, Ontario, Canada (Mizelle & Donahue 1944); Swamp Pools and Bayous near Tremont, La. (Seamster 1948). *Ameiurus natalis* (LeSueur), Myakka River, Fla., and Lake Okeechobee, Fla. (Mueller 1936a); Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943).

Ameiurus nebulosus (LeSueur), Myakka River, Fla., Lake Okeechobee, Fla. (Mueller 1936a); Oneida Lake, N. Y. (Mueller 1937); Dixon, Proulx, and Smoke lakes (all) Algonquin Park, Ontario, Canada (Mizelle & Donahue 1944); Yellow River Flowage next to Fisheries Laboratory near Spooner, Wis. (Mizelle & Regensberger 1945); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b). *Ictalurus furcatus* (LeSueur), Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943). *Ictalurus l. lacustris* (Walbaum), Upper Lake Pepin, Miss. River, (both) Wis. (Mizelle & Webb 1953; Mizelle & Klucka 1953).

C. RARUS Mizelle, 1940.—*Micropterus punctulatus* (Rafinesque), Cove Creek, Caryville, Tenn. (Mizelle 1940a).

C. ROBUSTUS Mueller, 1934 (Syn. *Cleidodiscus incisor* Mizelle, 1936; *Actinocleidus incisor* (Mizelle, 1934) as used by Mueller 1937 and *A. incisor* (Mizelle 1936) as used by Summers & Bennett 1938).—*Lepomis gibbosus* (Linnaeus), State Fish Hatchery Reservoir, Constantia, N. Y. (Mueller 1934); Syracuse, N. Y. (Mueller 1936); Island Lake near Spooner, Wis. (Mizelle & Regensberger 1945). *Chaenobryttus coronarius* (Bartram), Westhampton Lake, Univ. of Richmond, Va. (Hargis 1952b). *Lepomis cyanellus* Rafinesque, Hatchery Ponds, London, Ohio (Mueller 1936); Embarrass River, Urbana, Ill. (Mizelle 1938a); Urbana, Ill. (Kimpel 1939). *Lepomis macrochirus* Rafinesque, Hatchery Ponds at London, Ohio (Mueller 1936); Illinois River, Havana, Ill., Chautauqua Lake, Havana, Ill., Lake Decatur, Decatur, Ill., Horseshoe Lake, Cairo, Ill., Lake Senachwine, Henry, Ill. (Mizelle 1936); Baton Rouge and New Roads, La. (Summers & Bennett 1938); Reelfoot Lake, Tiptonville, Tenn., Lake Okeechobee, Moore Haven, Fla. (Mizelle & Brennan 1942); Chetac Lake near Birchwood, Wis., Yellow River Flowage next to Fisheries Laboratory near Spooner, Wis., Carrol Lake and Minocqua Thoroughfare along Woodruff Hatchery (both) near Woodruff, Wis. (Mizelle & Regensberger 1945); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b). "Sunfish" and "Bass," Hatching Ponds near Syracuse, N. Y. (Mueller 1936).

C. STENTOR Mueller, 1937.—*Ambloplites rupestris* (Rafinesque), Constantia, N. Y. (Mueller 1937); Yellow River Flowage next to Fisheries Laboratory near Spooner, Wis., Blue Lake near Minocqua, Wis. (Mizelle & Regensberger 1945). *Pomoxis nigro-maculatus* (LeSueur), Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b).

C. UNIFORMIS Mizelle, 1936.—*Pomoxis annularis* Rafinesque, Lake Decatur, Decatur, Ill. (Mizelle 1936); Salt Fork of Big Vermilion River south of Oakwood, Ill., Boomer Creek, Stillwater, Okla. (Mizelle 1938a). Reelfoot Lake, Tiptonville, Tenn., Miss. River in Ill. (Mizelle, LaGrave, & O'Shaughnessy 1943).

C. VANCLEAVEI Mizelle, 1936. (Syn. *Onchocleidus formosus* Mueller, 1936; *Cleidodiscus formosus* (Mueller, 1936) Price, 1937).—*Pomoxis annularis* Rafinesque, Lake Decatur, Decatur, Ill. (Mizelle, 1936); Salt Fork of Big Vermilion River, south of Oakwood, Ill., Boomer Creek, Stillwater, Okla. (Mizelle 1938a); Local Ponds and Streams near Stillwater, Okla. (Seamster

1938); Baton Rouge and New Roads, La. (Summers & Bennett 1938). Reelfoot Lake, Tiptonville, Tenn., Miss. River in Ill. (Mizelle, LaGrave, & O'Shaughnessy 1943), Miss. River in Buffalo Co., Wis. (Mizelle & Webb 1953). *Pomoxis nigro-maculatus* (LeSueur), Lake Okeechobee, Clewiston, Fla. (Mueller 1936a); Local Ponds and Streams near Stillwater, Okla. (Seamster 1938); Lake Decatur, Decatur, Ill., Salt Fork of Big Vermilion River south of Oakwood, Ill., Boomer Creek, Stillwater, Okla. (Mizelle 1938a); Reelfoot Lake, Tiptonville, Tenn., Miss. River in Ill., (Mizelle, LaGrave, & O'Shaughnessy 1943); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b).

C. VENARDI Mizelle & Jaskoski, 1942.—*Lepomis miniatus* Jordan, Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Jaskoski 1942).[3]

MURRAYTREMA Price, 1937

Diagnosis—Cephalic glands opening to exterior through four pairs of head organs. Haptor large, with two pairs of large hooks separated by three transversely placed nonarticulate bars; fourteen marginal hooklets. Intestinal branches not uniting posteriorly. Eyes present. Testis and ovary in equatorial zone. Cirrus with accessory piece. Vagina present, opening ventrally and medially.

Type species.—*Murraytrema robusta* (Murray, 1931) Price, 1937.

M. COPULATA Mueller, 1938. *Catostomus commersonii* (Lacépède), Chautauqua Lake, French Creek near Panama, (both) N. Y. (Mueller 1938); Silver Creek, Fond du Lac, Wis., St. Croix River, Burnett Co., Wis. (Mizelle & Klucka 1953). *Catostomus fecundus* Cope and Yarrow, Spring Lake, Wyo. (Mizelle & Webb 1953). *Hypentelium nigricans* (LeSueur), Chautauqua Lake, French Creek near Panama, (both) N. Y. (Mueller 1938). *Moxostoma anisurum* (Rafinesque) Chautauqua Lake, French Creek near Panama, (both) N. Y. (Mueller 1938). *Moxostoma aureolum* (LeSueur), Silver Creek, Fond du Lac Co., Wis., St. Croix River, Burnett Co., Wis. (Mizelle & Klucka 1953). *Moxostoma erythrurum* (Rafinesque), Chautauqua Lake, French Creek, near Panama, (both) N. Y. (Mueller 1938).

UROCLEIDUS Mueller, 1934, Emended Mizelle and Hughes, 1938

Synonyms—*Onochocleidus* Mueller, 1936, in part; *Tetracleidus* Mueller, 1936, in part; *Aristocleidus* Mueller, 1936, in part; *Haplocleidus* Mueller, 1937, in part; and *Pterocleidus* Mueller, 1937, in part.

Diagnosis—Tetraonchinae with trunk, eyes, gut, gonads, vitellaria, and haptoral bars as described for *Cleidodiscus*. Cirrus a cuticularized tube, straight or undulate with or without a cirral thread or fin, infrequently corkscrew-like. Accessory piece never basally articulated with the cirrus. Vagina, when present, opening on the right margin near midlength of trunk. Haptor generally distinct, subhexagonal; armed with two pairs of anchors and seven pairs of hooks.

---

[3] *C. chavarriai* and *C. travossosi* were described from the Costa Rican host *Rhamdia rogersi* (Regan) by Price in 1938.

One pair of anchors dorsal, the other pair ventral, in position. Parasitic on gills of freshwater fishes.

Type species—Urocleidus ferox Mueller, 1934.

Urocleidus includes species from the old genera *Aristocleidus, Haplocleidus, Onchocleidus, Pterocleidus, Tetracleidus,* and *Urocleidus* as originally defined (Mueller 1934, 1936, 1936a, 1937). After reviewing the species involved, it is considered sound to retain all of them in the genus *Urocleidus* Mueller, 1934, as emended by Mizelle and Hughes (1938), for the following reasons. Originally *Tetracleidus* was distinguished from *Urocleidus* by the presence of a vagina and from *Onchocleidus* in the possession of an accessory piece in the copulatory complex (Mueller 1936). Since in three of the six species (*U. dispar, U. mimum, U. similis*) originally described in *Onchocleidus* a vagina was not observed, and further an accessory piece has been observed in practically every species of *Onchocleidus* and probably exists in all of them, it is obvious that all of the forms in these three categories belong to a single genus, namely, *Urocleidus,* which has priority. *Aristocleidus* was proposed to include species essentially like those of *Tetracleidus* except for a discrepancy in the shape of the dorsal and ventral anchors (Mueller 1936a). Since discrepancies in anchor shape also occur in *Cleidodiscus brachus* and *Actinocleidus* species (*A. oculatus, A. recurvatus, A. scapularis*), *Aristocleidus* has no validity and becomes a synonym (in part) of *Urocleidus.* The old genus *Pterocleidus* Mueller, 1937, was distinguished as embracing *Onchocleidus*-like forms which possessed a "flat blade" arising near the distal end of each anchor shaft on the concave surface. Superficially this old category appears valid but the character involved is hardly of subgeneric much less generic level and in the authors' opinion cannot be used for generic fission any more than the widespread occurrence of a spine on the posterior border of the haptoral bars of Tetraonchinae. Further, *U. distinctus, U. torquatus,* etc. present an enlargement at the same point (as in "Pterocleidus" forms) on each anchor shaft and may be considered as intergrading between species with smooth, and those with a projection on each, anchor shaft. Similarly the old genus *Haplocleidus* Muellter, 1937, which was separated from *Onchocleidus* because of the larger size of the dorsal pair of anchors is without validity since *Cleidodiscus pricei* and *Urocleidus chautauquensis* possess anchors with size discrepancies which intergrade with the condition cited as the chief character of *Haplocleidus.* Hargis (1952) was convinced that the old genus *Haplocleidus* was valid and reinstated it but presently realizes that this group "is not a sound genus."[4]

The foregoing conclusions concerning the old genera *Aristocleidus, Haplocleidus* and *Pterocleidus* are based on the premise that genera must be separated by characters of more than insignificant magnitude. Generic fission for mere convenience of the novice or because of the presence of a relatively large number of species contained in a given genus, is considered inexcusable.

"Haplocleidus" species are indicated with a †, and those of "Pterocleidus" with a ‡ in the following list.

‡U. ACER (Mueller, 1936) Mizelle & Hughes, 1938. (Syn. *Onchocleidus*

[4] Private correspondence.

acer Mueller, 1936; *Pterocleidus acer* (Mueller, 1936) Mueller, 1937).—*Lepomis gibbosus* (Linnaeus), Cross Lake, N. Y. (Mueller 1936); Lake Senachwine, Henry, Ill. (Mizelle 1936). *Lepomis humilis* (Girard), Lake Senachwine, Henry, Ill. (Mizelle 1936). *Lepomis macrochirus* Rafinesque, Chautauqua Lake, Havana, Ill., Illinois River, Havana, Ill., Horseshoe Lake, Cairo, Ill., Lake Decatur, Decatur, Ill., Lake Senachwine, Henry, Ill., State Natural History Survey Pond, Urbana, Ill. (Mizelle 1938a); Local Ponds and Streams near Stillwater, Okla. (Seamster 1938); Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Brennan 1942); Madeline Lake near Woodruff, Wis. (Mizelle & Regensberger 1945); Swamp Pools and Bayous near Tremont, La. (Seamster 1948).

‡U. ACUMINATUS (Mizelle 1936) Mizelle & Hughes, 1938. (Syn. *Onchocleidus acuminatus* Mizelle, 1936; *Pterocleidus acuminatus* (Mizelle, 1936) Mueller, 1937).—*Lepomis megalotis* (Rafinesque), Embarrass River, Urbana, Ill. (Mizelle 1936); Swamp Pools and Bayous near Tremont, La. (Seamster 1948).

U. ADSPECTUS Mueller, 1936.—*Perca flavescens* (Mitchill), Cross Lake, N. Y. (Mueller 1936); Long, Opeongo, and Proulx lakes, (all) Algonquin Park, Ontario, Canada (Mizelle & Donahue 1944); Madeline Lake near Woodruff, Wis., Pinkeye Lake near Land O' Lakes, Wis. (Mizelle & Regensberger 1945).

†U. AFFINIS (Mueller, 1937) Mizelle & Hughes, 1938 (Syn. *Haplocleidus affinis* Mueller, 1937).—*Lepomis gibbosus* (Linnaeus), Fla. (Mueller 1937).

U. ANGULARIS Mueller, 1934 (Syn. *Ancyrocephalus angularis* (Mueller, 1934) Mueller, 1936).—*Fundulus diaphanus menona* Jordan & Copeland, Oneida Lake, N. Y. (Mueller 1934). *Fundulus diaphanus* (LeSueur), Oneida Lake, N .Y. (Mueller 1936).

U. ATTENUATUS Mizelle, 1941—*Lepomis microlophus* (Günther), Englewood Pond, Englewood, Fla., Everglades Canal, Naples, Fla., Lake Okeechobee, Moore Haven, Fla. (Mizelle 1941a); Canal, North Everglades, Fla. (Mizelle & Brennan 1942); Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943). *Lepomis macrochirus* Rafinesque, Canal, North Everglades, Fla. (Mizelle & Brennan 1942). *Lepomis miniatus* Jordan, Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Jaskoski 1942).

‡U. BIRAMOSUS (Mueller, 1937) Mizelle & Hughes, 1937 (Syn. *Pterocleidus biramosus* Mueller, 1937).—*Lepomis macrochirus* Rafinesque, Fla. (Mueller 1937); Lake Okeechobee, Moore Haven, Fla. (Mizelle & Brennan 1942).

U. CHAENOBRYTTUS Mizelle & Seamster, 1939.—*Chaenobryttus coronarius* (Bartram), Roadside Canal, Naples, Fla., Roadside Ditch, Englewood, Fla., Woodmere Pond, Englewood, Fla. (Mizelle & Seamster 1939); Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943); Westhampton Lake, Univ. Richmond, Va. (Hargis, 1952b). *Lepomis macrochirus* Rafinesque, Westhampton Lake. Univ. Richmond, Va. (Hargis 1952b). *Lepomis miniatus* Jordan, Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Jaskoksi 1942).

U. CHAUTAUQUENSIS (Mueller, 1938) Mizelle & Hughes, 1938 (Syn. *Tetracleidus chautauquaensis* Mueller, 1938; *Cleidodiscus chautauquaensis* Mueller, 1938).—*Ambloplites rupestris* (Rafinesque), Chautauqua Lake, N. Y. (Mueller 1938); Yellow River Flowage next to Fisheries Laboratory near Spooner, Wis. (Mizelle & Regensberger 1945).

U. CHRYSOPS Mizelle & Klucka, 1953.—*Lepibema chrysops* (Rafinesque), Upper Lake Pepin, Miss. River, (both) Wis. (Mizelle & Klucka 1953); Upper Lake Pepin, Miss. River, (both) Fountain City, Buffalo Co., Wis. (Mizelle & Webb 1953).

U. CYANELLUS (Mizelle, 1938) Mizelle & Hughes, 1938 (Syn. *Onchocleidus cyanellus* Mizelle, 1938).—*Lepomis cyanellus* Rafinesque, Embarrass River, Urbana, Ill. (Mizelle 1938); Local Ponds and Streams near Stillwater, Okla. (Seamster 1938).

†U. DISPAR (Mueller, 1936) Mizelle & Hughes, 1938 (Syn. *Onchocleidus dispar* Mueller, 1936; *Haplocleidus dispar* (Mueller, 1936) Mueller, 1937).—*Lepomis gibbosus* (Linnaeus), Constantia, N. Y. (Mueller 1936); Long, Opeongo, and Proulx lakes (all) Algonquin Park, Ontaria, Canada (Mizelle & Donahue 1944); Westhampton Lake, Univ. Richmond, Va. (Hargis, 1952b). *Chaenobryttus coronarius* (Bartram), Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b). *Lepomis humilis* (Girard), Local Ponds and Streams near Stillwater, Okla. (Seamster 1938). *Lepomis macrochirus* Rafinesque, Local Ponds and Streams near Stillwater, Okla. (Seamster 1938); Chautauqua Lake, Havana, Ill., Illinois River, Havana, Ill., Horseshoe Lake, Cairo, Ill., Lake Decatur, Decatur, Ill., and Lake Senachwine, Henry, Ill. (Mizelle 1938a); Chetac Lake near Birchwood, Wis., Bass Lake (Hatchery) near Woodruff, Wis. (Mizelle & Regensberger 1945); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b). *Micropterus salmoides* (Lacépède), Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943).

U. DISTINCTUS (Mizelle, 1936) Mizelle & Hughes, 1938 (Syn. *Onchocleidus distinctus* Mizelle 1936).—*Lepomis megalotis* (Rafinesque), Embarrass River, Urbana, Ill. (Mizelle 1936).

U. DOLORESAE Hargis 1952.—*Chaenobryttus coronarius* (Bartram), Westhampton Lake, Univ. Richmond, Va. (Hargis 1952a).

U. FEROX Mueller, 1934 (Syn. *Onchocleidus ferox* (Mueller, 1934) Mueller, 1936; *Onchocleidus mucronatus* Mizelle, 1936; *Urocleidus mucronatus* (Mizelle, 1936) Mizelle & Hughes 1938).—*Lepomis gibbosus* (Linnaeus), Oneida Lake, N. Y. (Mueller 1934), Constantia, N. Y. (Mueller 1936); Lake Senachwine, Henry, Ill. (Mizelle 1936). Brewer, Costello, Long, Opeongo, and Proulx (all) Algonquin Park, Ontario, Canada (Mizelle & Donahue 1944); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b). *Chaenobryttus coronarius* (Bartram), Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b). *Lepomis humilis* (Girard), Lake Senachwine, Henry, Ill., Salt Fork of Big Vermilion River, Homer, Ill. (Mizelle 1936); Local Ponds and Streams near Stillwater, Okla. (Seamster 1938). *Lepomis macrochirus* Rafinesque, Lake Decatur, Decatur, Ill., State Natural History Survey Pond, Urbana, Ill., Lake Senachwine, Henry, Ill. (Mizelle 1936); Boomer Creek,

Stillwater, Okla., Lake Chautauqua, Havana, Ill. (Mizelle 1938a); Local Ponds and Streams near Stillwater, Okla. (Seamster 1938); Baton Rouge and New Roads, La. (Summers & Bennett 1938); Reelfoot Lake, Tiptonville, Tenn., Lake Okeechobee, Moore Haven, Fla. (Mizelle & Brennan 1942); Bass Lake (Hatchery), Carrol Lake, Madeline Lake, Minocqua Thoroughfare along Woodruff Hatchery (all) near Woodruff, Wis., Chetac Lake near Birchwood, Wis., Yellow River Flowage next to Fisheries Laboratory near Spooner, Wis. (Mizelle & Regensberger 1945); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952a). Hybrids *Lepomis gibbosus* X *L. humilis* and *Lepomis gibbosus* X *L. macrochirus*, Lake Senachwine, Henry, Ill. (Mizelle 1936).

U. FUNDULUS Mizelle, 1940.—*Fundulus catenatus* (Storer), Cove Creek, Caryville, Tenn. (Mizelle 1940a)

†U. FURCATUS (Mueller, 1937) Mizelle & Hughes, 1938 (Syn. *Haplocleidus furcatus* Mueller, 1937).—*Micropterus salmoides* (Lacépède,), Fla. (Mueller 1937); Baton Rouge, La. (Summers & Bennett 1938); Hatchery, Norris, Tenn. (Mizelle 1940); Chetac Lake near Birchwood, Wis., Bass Lake (Hatchery) near Woodruff, Wis. (Mizelle & Regensberger 1945); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b). *Micropterus punctulatus* (Rafinesque), Norris Lake, Norris, Tenn., Cold Creek below Norris Dam (Tenn.) (Mizelle 1940).

‡U. GRANDIS Mizelle & Seamster, 1939.—*Chaenobryttus coronarius* (Bartram), Roadside Canal, Naples, Fla., Woodmere Pond, Englewood, Fla. (Mizelle & Seamster 1939); Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943).

U. HELICIS (Mueller, 1936) Mizelle & Hughes, 1938 (Syn. *Onchocleidus helicis* Mueller, 1936).—*Micropterus salmoides* (Lacépède), Cross Lake, N. Y. (Mueller 1936). *Lepomis gibbosus* (Linnaeus), Bullhead Lake near Minocqua, Wis., Minocqua Thoroughfare along Woodruff Hatchery near Woodruff, Wis. (Mizelle & Regensberger 1945).

U. INTERRUPTUS (Mizelle, 1936) Mizelle and Hughes, 1938 (Syn. *Onchocleidus interruptus* Mizelle, 1936).—*Morone interrupta* Gill, Lake Decatur, Decatur, Ill., Lake Senachwine, Henry, Ill. (Mizelle 1936).

U. MALLEUS (Mueller, 1938) Mizelle & Hughes, 1938 (Syn. *Cleidodiscus malleus* Mueller, 1938).—*Percina caprodes* (Rafinesque) and *Hadropterus maculatus* (Girard), Chautauqua Lake, N. Y. (Mueller 1938).

U. MIMUS (Mueller, 1936) Mizelle and Hughes, 1938 (Syn. *Onchocleidus mimus* Mueller, 1936).—*Esox reticulatus* LeSueur, London, Ohio (Mueller 1936). *Lepibema chrysops* (Rafinesque), London, Ohio (Mueller 1936); Oneida Lake, N. Y. (Mueller 1937); Lake Pepin, Miss. River, (both) Wis. (Mizelle & Klucka 1953); Miss. River, Fountain City, Buffalo Co., Wis. (Mizelle & Webb 1953).

‡U. MINIATUS Mizelle & Jaskoski, 1942.—*Lepomis miniatus* Jordan, Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Jaskoski 1942).

U. MOOREI Mizelle, 1940.—*Poecilichthys flabellaris* (Rafinesque), Cold Creek near Norris Dam, Tenn. (Mizelle 1940a).

†U. PARVICIRRUS Mizelle and Jaskoski, 1942.—*Lepomis miniatus* Jordan, Reelfoot Lake, Tiptonville, Tenn. (Mizelle and Jaskoski 1942). *Lepomis microlophus* (Günther), Reelfoot Lake, Tiptonville, Tenn. (Mizelle and Cronin 1943).

U. PERDIX (Mueller, 1937) Mizelle & Hughes, 1938 (Syn. *Onchocleidus perdix* Mueller, 1937).—*Lepomis macrochirus* Rafinesque, Fla. (Mueller 1937).

U. PRINCIPALIS (Mizelle, 1936) Mizelle and Hughes, 1938 (Syn. *Onchocleidus principalis* Mizelle, 1936; *Onchocleidus contortus* Mueller, 1937).—*Micropterus punctulatus* (Rafinesque), Salt Fork of Big Vermillion River, Homer, Ill. (Mizelle 1936); Cove Creek, Caryville, Tenn., Norris Lake, Norris, Tenn., Cold Creek below Norris Dam (Tenn.) (Mizelle 1940). *Micropterus dolomieu* Lacépède, Local Ponds and Streams near Stillwater, Okla. (Seamster 1938); Salt Fork of Big Vermillion River, Homer, Ill. (Mizelle 1938a); Cove Creek, Caryville, Tenn. (Mizelle 1940). *Micropterus salmoides* (Lacépède), Fla. (Mueller, 1937); Baton Rouge, La. (Summers and Bennett 1938); Lake Senachwine, Henry, Ill. (Mizelle 1938a); Hatchery, Norris, Tenn. (Mizelle 1940); Reelfoot Lake, Tiptonville, Tenn. (Mizelle and Cronin 1943); Bass Lake (Hatchery) near Woodruff, Wis., Chetac Lake near Birchwood, Wis. (Mizelle and Regensberger 1945); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b).

U. PROCAX Mizelle & Donahue, 1944.—*Lepomis gibbosus* (Linnaeus), Long and Opeongo lakes in Algonquin Park, Ontario, Canada (Mizelle & Donahue 1944); Westhampton Lake, Univ. Richmond, Va. (Hargis 1952b).

U. SECULUS Mizelle & Arcadi, 1945.—*Gambusia a. affinis* (Baird & Girard), San Gabriel River, near Whittier, Calif. (Mizelle & Arcadi 1945); Swamp Pools and Bayous near Tremont, La. (Seamster 1948).

U. SIMILIS (Mueller, 1936) Mizelle & Hughes, 1938 (Syn. *Onchocleidus similis* Mueller, 1936).—*Lepomis gibbosus* (Linnaeus), Cross Lake, N. Y. (Mueller 1936).

U. SPIRALIS (Mueller, 1937) Mizelle & Hughes, 1938 (Syn. *Onchocleidus spiralis* Mueller, 1937).—*Lepomis gibbosus* (Linnaeus), Fla. (Mueller 1937).

U. TORQUATUS Mizelle & Cronin, 1943.—*Lepomis microlophus* (Günther) Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943).

U. UMBRAENSIS Mizelle, 1938—*Fundulus notatus* (Rafinesque), Embarrass River, Urbana, Ill., Kaskaskia River, Bondville, Ill. (Mizelle 1938). *Fundulus dispar* (Agassiz), Baton Rouge, La. (Summers & Bennett 1938).

U. VARIABILIS Mizelle & Cronin, 1943.—*Lepomis microlophus* (Günther), Reelfoot Lake, Tiptonville, Tenn. (Mizelle & Cronin 1943).

‡U. WADEI Seamster, 1948.—*Centrarchus macropterus* (Lacépède), Swamp Pools and Bayous near Tremont, La. (Seamster 1948).[5]

---

[5] Mueller (1936a) described *U. hastatus* (Syn. *Aristocleidus hastatus*) from the marine host *Roccus lineatus* (Bloch) taken from Peace River near Fort Ogden, Fla. There have been no additional reports for this parasite.

TETRAONCHUS Diesing, 1858

Diagnosis.—Cephalic glands opening to exterior through several pair of head organs. Haptor more or less distinctly set off from body proper, with 2 pairs of large hooks supported by a single large transverse cuticular bar; 16 marginal hooklets. Intestine single, without diverticula. Eyes present. Testis and ovary in equatorial zone. Vagina absent. (quoted from Price, 1937)

Type species.—*Tetraonchus monenteron* (Wagener, 1857) Diesing, 1858.

T. monenteron (Wagener, 1857) (Syn. *Dactylogyrus monenteron* Wagener, 1857; *Gyrodactylus cochlea* Wedl, 1857; *Monocoelium monenteron* (Wagener, 1857) Wegener, 1909; *Ancyrocephalus monenteron* Lühe, 1909).—*Esox lucius* Linnaeus, Various localities in Eurasia (Wagener 1857, Wedl 1857, Diesing 1858, Parona & Perugia 1890, Olsson 1893, Lühe 1909, Wegener, 1909, Vlassenko 1928, Bychowsky 1929, 1933, Dogiel & Bychowsky 1933, Dogiel & Petruschewsky, 1933, I. Bychowsky 1936, Alarotu 1944); Oneida Lake, N. Y. (Van Cleave & Mueller 1934); Yellow River Flowage next to Fisheries Laboratory near Spooner, Wis., Thoroughfare along Woodruff Hatchery near Woodruff, Wis. (Mizelle & Regensberger 1945).

T. RAUSCHI Mizelle & Webb, 1953.—*Thymallus signifer* Richardson, Anaktuvak Pass, Alaska (Mizelle & Webb 1953).

T. VARIABILIS Mizelle & Webb, 1953.—*Prosopium w. williamsi* (Girard), Snake River, Wyo., (Mizelle & Webb 1953); *Prosopium cylindraceum quadrilaterale* (Richardson). Tolugak Lake and Anaktuvak Pass, Alaska (Mizelle & Webb 1953).[6]

HOSTS AND INFECTING SPECIES

AMEIURIDAE

Ameiurus melas Rafinesque.—*Cleidodiscus floridanus, C. pricei.* **Ameiurus natalis** LeSueur).—*Cleidodiscus pricei.* **Ameiurus nebulosus** LeSueur.—*Cleidodiscus pricei.* **Ictalurus furcatus** (LeSueur).—*Cleidodiscus floridanus, C. pricei.* **Ictalurus l. lacustris** (Walbaum).—*Cleidodiscus floridanus, C. pricei.* **Ictalurus lacustris punctatus** (Rafinesque).—*Cleidodiscus floridanus, C. pricei.* **Pilodictis olivaris** (Rafinesque).—*Cleidodiscus floridanus.*

CATOSTOMIDAE

Catostomus commersonii (Lacépède).—*Murraytrema copulata.* **Catostomus fecundus** Cope & Yarrow.—*Murraytrema copulata.* **Hypentelium nigricans** (LeSueur).—*Murraytrema copulata.* **Moxostoma anisurum** (Rafinesque).—*Murraytrema copulata.* **Moxostomun aureolum.**—*Murraytrema copulata.* **Moxostoma erythrurum** (Rafinesque).—*Murraytrema copulata.*

[6] Price (1937) described *T. alaskensis* from *Salmo mykiss* Walbaum, *Salvelinus malma spectabilis* (Girard) and *Onchorhynchus kisutch* (Walbaum) taken from Sitkoh Bay, Alaska.

CENTRARCHIDAE

Ambloplites rupestris (Rafinesque).—*Cleidodiscus alatus C. megalonchus, C. stentor, Urocleidus chautauquaensis.* **Centrarchus macropterus** (Lacépède).—*Urocleidus wadei.* **Chaenobryttus coronarius** (Bartram).—*Actinocleidus fergusoni, A. flagellatus, A. okeechobeensis, Cleidodiscus robustus, Urocleidus chaenobryttus, U. dispar, U. doloresae, U. ferox, U. grandis.* **Lepomis cyanellus** Rafinesque.—*Actinocleidus longus, Cleidodiscus diversus, C. robustus, Urocleidus cyanellus.* **Lepomis gibbosus** (Linnaeus).—*Actinocleidus gibbosus, A. incus, A. maculatus, A. oculatus, A. recurvatus, A. scapularis, A. sigmoideus, Cleidodiscus megalonchus, C. nematocirrus, C. robustus, Urocleidus acer, U. affinis, U. dispar, U. ferox, U. helicis, U. procax, U. similis, U. spiralis.* Hybrids: **Lepomis gibbosus X L. humilis, L. gibbosus X L. macrochirus.**—*Urocleidus ferox.* **"Sunfish."**—*Actinocleidus oculatus, Cleidodiscus robustus.* **Lepomis humilis** (Girard).—*Actinocleidus fergusoni, Urocleidus acer, U. dispar, U. ferox.* **Lepomis macrochirus** Rafinesque.—*Anchoradiscus anchoradiscus, Actinocleidus fergusoni, A. gracilis, A. longus, A. oculatus, Clavunculus bursatus, Cleidodiscus nematocirrus, C. robustus, Urocleidus acer, U. attenuatus, U. biramosus, U. chaenobryttus, U. dispar, U. ferox, U. perdix.* **Lepomis megalotis** (Rafinesque).—*Actinocleidus articularis, Cleidodiscus bedardi, C. nematocirrus, Urocleidus acuminatus, U. distinctus.* **Lepomis microlophus** (Günther).—*Anchoradiscus anchoradiscus, Actinodiscus bakeri, A. bifidus, A. crescentis, A. harquebus, A. maculatus, Clavunculus bifurcatus, Cleidodiscus nematocirrus, Urocleidus attenuatus, U. parvicirrus, U. torquatus, U. variabilis.* **Lepomis miniatus** Jordan.—*Actioncleidus brevicirrus, A. subtriangularis, Cleidodiscus chelatus, C. venardi, Urocleidus attenuatus, U. chaenobryttus, U. miniatus, U. parvicirrus.* **Lepomis symmetricus** Forbes.—*Anchoradiscus triangularis.* **Micropterus dolomieu** Lacépède.—*Actinocleidus fusiformis, Clavunculus bursatus, Cleidodiscus banghami, C. megalonchus, Urocleidus principalis.* **Micropterus punctulatus** (Rafinesque)—*Actinocleidus fusiformis Clavunculus bursatus, Cleidodiscus banghami, C. rarus, Urocleidus furcatus, U. principalis.* **Micropterus salmoides** (Lacépède).—*Actinocleidus fusiformis, Clavunculus bursatus, C. unguis, Urocleidus dispar, U. furcatus, U. helicis, U. principalis.* **"Bass."**—*Cleidodiscus robustus.* **Pomoxis annularis** Rafinesque.—*Cleidodiscus capax, C. longus, C. uniformis, C. vancleavei.* **Pomoxis nigromaculatus** (LeSueur).—*Cleidodiscus capax, C. stentor, C. vancleavei.*

COREGONIDAE

Prosopium cylindraceum quadrilaterale (Richardson).—*Tetraonchus variabilis.* **Prosopium w. williamsoni** (Girard).—*Tetraonchus variabilis.*

CYPRINIDAE

Margariscus margarita (Cope).—*Cleidodiscus brachus.* **Semotilus atromaculatus** (Mitchill).—*Cleidodiscus brachus.*

CYPRINODONTIDAE

Fundulus catenatus (Storer).—*Urocleidus fundulus.* **Fundulus d. diaphanus** (LeSueur).—*Urocleidus angularis.* **Fundulus diaphanus menona** Jordan and Copeland.—*Urocleidus angularis.* **Fundulus dispar** (Agassiz).—*Urocleidus umbraensis.* **Fundulus notatus** (Rafinesque).— *Urocleidus umbraensis.*

ESOCIDAE

Esox lucius Linnaeus.—*Tetraonchus monenteron.* **Esox reticulatus** LeSueur.—*Urocleidus mimus.*

PERCIDAE

Hadropterus maculatus (Girard).—*Urocleidus malleus.* **Percina caprodes** (Rafinesque).—*Urocleidus malleus.* **Perca flavescens** (Mitchill).—*Urocleidus adspectus.* **Poecilichthys flabellaris** (Rafinesque).—*Urocleidus moorei.* **Stizostedion vitreum** (Mitchill).—*Cleidodiscus aculeatus.*

POECILIIDAE

Gambusia a. affinis (Baird and Girard).—*Urocleidus seculus.*

SALMONIDAE

Onchorhynchus kisutch (Walbaum).—*Tetraonchus alaskensis.* **Salmo clarkii** Richardson.—*Tetraonchus alaskensis.* **Salvelinus malma spectabilis** (Girard).—*Tetraonchus alaskensis.*

SERRANIDAE

Lepibema chrysops (Rafinesque).—*Urocleidus chrysops, U. mimus.* **Morone interrupta** Gill.—*Urocleidus interruptus.*

THYMALLIDAE

Thymallus signifer Richardson.—*Tetraonchus rauschi.*

REFERENCES

ALAROTU, H. 1944—Untersuchungen über die an Fischen in Finnland lebenden monogenetischen Trematoden. Acta Zool. Fenn. 43:1-52.

BYCHOWSKY, B. 1929—Trematoden der Fische in der Umgebund der Stadt Kostroma. Trav. Soc. Nat. Leningrad 59:3-27.

———1933—Beitrag zur Kenntnis neuer monogenetischer Fischtrematoden aus dem Kaspisee nebst einigen Bemerkungen über die Systematik der Monopisthodiscinea Fuhrmann 1928. Zool. Anz. 105(½):17-38.

BYCHOWSKI, I. 1936—Zur Kenntnis der Parasitenfauna der Fische Karelien.—II. Die Parasiten der Fischer der Kleinen Waldseen s. g. "Lamben." Berichte Borodin Stat. 8:123-138.

COOPER, A. R. 1915—Trematodes from marine and fresh-water fishes, including one species of ectoparasitic turbellarian. Trans. Roy. Soc. Canada 9(3):181-205.

DIESING, K. M. 1858—Revision der Myzhelminthen. S.B. Akad. Wiss. Wien. 32(23): 307-390.

DOGIEL, V. AND B. BYCHOWSKY 1933—Fischparasitenfauna Aralsee. Mag. Parasit. Leningrad 4:241-345.

——— AND G. K. PETRUSCHEWSKY 1933—Die Parasitäre fauna der Fische aus der Newabucht. Trav. Soc. Nat. Leningrad 62:366-434.

HARGIS, W. J., JR. 1952—A revision of the genera of the subfamily Tetraonchinae. Proc. Helm. Soc. Wash. 19(1):40-44.

———1952a—Monogenetic trematodes of Westhampton Lake fishes. I. Two new forms. Amer. Midl. Nat. 47(2):471-477.

———1952b—Monogenetic trematodes of Westhampton Lake fishes. II. A list of species and key to the genera encountered. Va. J. Sci. (new ser.) 3(2):112-115.

———1953—Monogenetic trematodes of Westhampton Lake fishes. III. Part 2. A discussion of host-specificity. Proc. Helm. Soc. Wash. 20(2):98-104.

KIMPEL, H. G. 1939—Studies on the taxonomy of the genus Neodactylogyrus, with descriptions of new species, and the immunity of fresh-water fishes to gill trematodes (Gyrodactyloidea). Private publication.

LÜHE, M. F. L. 1909—Parasitische Plattwurner.—1. Trematodes. Süsswasserfauna Deutschlands (Brauer) 17:1-217.

MIZELLE, JOHN D. 1936—New species of trematodes from the gills of Illinois fishes. Amer. Midl. Nat. 17(5):785-805.

———1938—New species of monogenetic flukes from Illinois fishes. *Ibid.* 19(2): 465-470.

———1938a—Comparative studies on trematodes (Gyrodactyloidea) from the gills of North American freshwater fishes. Ill. Biol. Monogr. 17:1-81.

———1940—Studies on monogenetic trematodes. III. Redescriptions and variations in known species. J. Parasit. 26(3):165-178.

———1940a—Studies on monogenetic trematodes. II. New species from Tennessee fishes. Trans. Amer. Micros. Soc. 59(3):285-289.

———1941—Studies on monogenetic trematodes. IV. Anchoradiscus, a new dactylogyrid genus from the bluegill and the stump-knocker sunfish. J. Parasit. 27(2):159-163.

———1941a—Studies on monogenetic trematodes. V. Tetraonchinae of the stump-knocker sunfish *Eupomotis microlophus* (Guenther). Amer. Midl. Nat. 26(1):98-104.

———1955—Studies on monogenetic trematodes. XIX. The status of North American Dactylogyrinae and Tetraonchinae. Proc. Ind. Acad. Sci. 64:260-264.

——— AND JOHN ARCADI 1945—Studies on monogenetic trematodes. XIII. *Urocleidus seculus*, a new species of tetraonchinae from the viviparous top minnow, *Gambusia affinis affinis* (Baird and Girard). Trans. Amer. Micro. Soc. 64(4):293-296.

——— AND WALTER J. BRENNAN 1942—Studies on monogenetic trematodes. VII. Species infesting the bluegill sunfish. Amer. Midl. Nat. 27(1):135-144.

——— AND JOHN P. CRONIN 1943—Studies on monogenetic trematodes. X. Gill parasites from Reelfoot Lake fishes. *Ibid.* 30(1):196-222.

——— AND M. A. DONAHUE 1944—Studies on monogenetic trematodes. XI. Dactylogyridae from Wisconsin fishes. *Ibid.* 49(3)720-733.

——— AND R. C. HUGHES 1938—The North American freshwater Tetraonchinae. *Ibid.* 20(2):341-353.

——— AND BENEDICT J. JASKOSKI 1942—Studies on monogenetic trematodes. VIII. Tetraonchinae infesting *Lepomis miniatus* Jordan. *Ibid.* 27(1):145-153.

——— AND A. R. KLUCKA 1953—Studies on monogenetic trematodes. XIV. Dactylogyridae from Wisconsin fishes. *Ibid.* 49(3):720-733.

———, D. R. LAGRAVE AND R. P. O'SHAUGHNESSY 1943—Studies on monogenetic trematodes. IX. Host specificity of Pomoxis Tetraonchinae. *Ibid.* 29(3):730-731.

——— AND REGIS REGENSBERGER 1945—Studies on monogenetic trematodes. XII. Dactylogyridae from Wisconsin fishes. *Ibid.* 34(3):673-700.

——— AND AARON SEAMSTER 1939—Studies on monogenetic trematodes. I. New species from the warmouth bass. J. Parasit. 25(6):501-507.

——— AND F. O. WEBB 1953—Studies on monogenetic trematodes. XV. Dactylogyridae from Alaska, Wisconsin and Wyoming fishes. Amer. Midl. Nat. 50(1):206-217.

MUELIER, J. F. 1934—Parasites of Oneida Lake fishes. Part 4. Additional notes on parasites of Oneida Lake fishes, including descriptions of new species. Roosevelt Wild Life Annals 3(4):335-373.

———1936—Studies on North American Gyrodactyloidea. Trans. Amer. Micros. Soc. 55(1):55-72.

———1936a—New gyrodactyloid trematodes from North American fishes. *Ibid.* 55(4): 457-464.

———1937—Further studies on North American Gyrodactyloidea. Amer. Midl. Nat. 18(2):207-219.

———1938—Additional species of North American Gyrodactyloidea (Trematoda). *Ibid.* 19(1):220-235.

OLSSON, P. 1893—Bidrag till skandinaviens helminthfauna. II. K. svenska Vetensk.-Akad. Handl. n.F. 14:1-35.

PARONA, C. AND A. PERUGIA 1890—Trematoda parassiti delle branchie dei pesci italiani. Atti. Soc. ligust. sci. nat. geogr. 1:59-70.

PRICE, E. W. 1937—A new monogenetic trematode from Alaskan salmonoid fishes. Proc. Helmin. Soc. Wash. 4(1):27-29.

———1937a—North American monogenetic trematodes. I. The superfamily Gyrodactyloidea. Jour. Wash. Acad. Sci. 27(3):114-130, and (4):146-164.

———1938—The monogenetic trematodes of Latin America. In Livro Jubilar Prof. Travassos. Rio de Janeiro, Brasil. 3:407-413.

SEAMSTER, A. 1938—Studies on gill trematodes from Oklahoma fishes. Amer. Midl. Nat. 20(3):603-612.

———1948—Gill parasites from Louisiana fishes with a description of *Urocleidus wadei* n. sp. *Ibid.* 39(1):165-168.

SPROSTON, NORA G. 1946—A synopsis of monogenetic trematodes. Trans. Zool. Soc. London 25, part 4, :185-600.

STAFFORD, J. 1905—Trematodes from Canadian vertebrates. Zool. Anz. 28(21-22):681-694.

SUMMERS, W. A. 1937—A new species of Tetraonchinae from *Lepomis symmetricus*. J. Parasit. 23:432-434.

——— AND H. J. BENNETT 1938—A preliminary survey of the trematodes from the gills of Louisiana fishes (abstract). Proc. La. Acad. Sci. 4(1):247-248.

VAN CLEAVE, H. J. AND J. F. MUELLER 1932—Parasites of Oneida Lake fishes. Part I. Descriptions of new genera and new species. Roosevelt Wild Life Annals 3(1): 1-72.

——— AND ——— 1934—Parasites of Oneida Lake fishes. Part III. A biological and ecological survey of the worm parasites. *Ibid.* 3(3):161-334.

VLASSENKO, N. M. 1928—Ankyrocotyle baikalense n. g., n. sp. Russ Hydrobiol. Z. 7:229-248.

WAGENER, G. R. 1857—Beiträge zur Entwicklungsgeschichte der Eingeweidewürmer. Naturk. Verhandel. Holl. Maatsch. Wetensch. Haarl.

WEDL, C. 1858—Anatomische Beobachtungen über Trematoden. S.B. Akad. Wiss. Wien d. Wissensch. Wien, Math-naturw. cl. 26(1):241-278.

WEGENER, G. 1909—Ektoparasiten der Fische Ostpreussens. Schrift d. Phys. Okon. Gesellsch. z. Königsberg 50:218-247.

A New Species of Rhamnocercinae

Aaron Seamster and Lawrence H. Monaco
Del Mar College, Corpus Christi, Texas

The subfamily Rhamnocercinae was erected by Monaco et al. (1954) as a result of recovering the type genus and species from a Pacific coast sciaenid. The present authors have discovered an additional species of this subfamily on two Gulf of Mexico sciaenids, *Micropogon undulatus* (L.) and *Menticirrhus littoralis* (Holbrook). The host material was collected from the South Jetty, Port Aransas, Texas and Bob Hall Pier on Padre Island near Corpus Christi, Texas. The gills were prepared for examination according to the method used by Mizelle (1936).

Rhamnocercus stichospinus n. sp.

Host and locality.—*Micropogon undulatus* (L.); South Jetty, Port Aransas, Texas.

Specimens studied.—Twenty.

Type specimens.—Type: U.S.N.M. Helm. Coll. No. 37497. Paratypes: U.S.N.M. Helm. Coll. No. 37498.

Description.—Relatively small dactylogyrid with thin cuticle and relatively short, anteriorly directed cuticular body spines along the posterior one fourth of the body. Total length 0.744 mm (0.590-0.990 mm); greatest body width 0.095 mm (0.060-0.140 mm) usually present in anterior body half. Eyespots four, members of posterior pair always larger and usually closer together than those of anterior pair. Accessory melanistic granules, apparently same type as those comprising eyespots, often present in vicinity of eyespots. Cephalic lobes two; head organs conspicuous. Pharynx subcircular to broadly ovate (transversely) in outline and 0.032 mm (0.030-0.033 mm) in greatest diameter. Peduncle relatively long, tapered posteriorly with six rows of spine-like hooks along entire length. Each peduncular hook composed of a rounded base, a relatively heavy shaft which tapers distally to a point, and an opposable piece. Lateral margins of shaft curved upward and toward mid-line of shaft. Peduncular hooks diminish in length in anterior direction (figs. 1-3). Haptor expanded laterally and more than twice as wide as the greatest body width. Haptor width approximately 0.285 mm (0.250-0.360 mm). A row of accessory spines situated dorsal and a row ventral to bars; individual spines diminish in length toward mid-haptoral line (fig. 16a, ventral row not shown) and each perforated near anterior end which occasionally appears frayed (figs. 4, 5). A single row of spines situated immediately anterior to ventral bar (fig. 16b). Two pairs of slightly curved accessory spines anterior to the row of spines above dorsal bars (fig. 16c). A clump of smaller spines appears lateral to each member of the posterior pair of last-named accessory spines (fig. 16d). Three haptoral bars present; ventral (fig. 8) longest with ends sharply tapered and gently curved, conspicuous longitudinal groove present, anterior border deeply notched at mid-length, posterior border with small tubercle opposite notch, length 0.172 mm (0.136-0.210 mm). Two dorsal bars (figs. 6, 7) of approximately equal size articulated to ventral bar; length 0.086 mm (0.073-0.095 mm). Anchors similar in shape, approximately equal in size and possessing solid bases and with slightly curved shafts and recurved points (figs. 10-13). Dorsal anchor with superficial root reduced and constricted near midportion to form rounded knob-like process, deep root well developed; dorsal anchor length 0.056 mm (0.042-0.065 mm); greatest width of base 0.010 mm (figs. 10, 11). Ventral anchors similar in shape to that of dorsal anchors but with superficial root more reduced; ventral anchor length 0.054 mm (0.045-0.063 mm); greatest width of base 0.010 mm (0.005-0.01 mm) (figs. 12, 13). Haptoral hooks 14 in number approximately equal in size and normal in arrangement (Mizelle 1938). Each hook composed of a gently curved shaft, a sickle-shaped termination, and opposable piece; hook base not dif-

ferentiated as such. Posteriorly projecting process arising on sickle-shaped termination, usually conspicuous. Hook lengths 0.011 mm (0.010-0.012 mm) (figs. 14, 15). Vitellaria heavily developed and extend from posterior margin of pharynx to anterior extremity of peduncle. Gonads not observed. Vagina on or near left margin near body mid-length. Copulatory complex composed of a cirrus; accessory piece lacking. Cirrus long, tubular, base expanded, tip slightly enlarged and bulbular in shape. Cirrus enclosed in a thin pellicle-like covering which appears to be expanded into two or more fin-shaped structures encircling base of cirrus. Cirrus length 0.071 mm (0.060-0.084 mm) (fig. 9).

Rhamnocercus stichospinus n. sp. possesses characteristics of the genus and is similar to the type species, *R. rhamnocercus* Monaco et al., 1954 in the following: (a) dorsal anchors of the latter species (op. cit., figs. 11, 12) are similar to those of the present species (figs. 12, 13), and (b) dorsal bars of *R. rhamnocercus* (op. cit., figs. 3, 4) resemble those of *R. stichospinus* (figs. 6, 7). Differences include: (a) cirrus enclosed in pellicle-like sheath (fig. 9), (b) edges of peduncular spines curved upward and inward (figs. 1-3), (c) accessory haptoral armament consisting of a single row of accessory spines on each haptoral surface adjacent to bars (fig. 16a), a single row anterior to dorsal bars (fig. 16b) and two pairs of ventral spines (fig. 16c), plus a lateral clump of spines situated near each member of the posterior pair of the last named spines (fig. 16d). (d) ventral bar sharply tapered at each end and deeply notched at mid-length (fig. 8), (e) dorsal anchor with superficial root constricted near mid-portion (figs. 10, 11), (f) no acicular internal spicules observed, and (g) individual spines of dorsal and ventral rows occasionally frayed (figs. 4, 5).

The present study also has revealed the following distribution records: *Pseudohaliotrema carbunculus* Hargis, 1955, from *Lagodon rhomboides* (L.); *Ancyrocephalus felix* Hargis, 1955, from *Galeichthys felis* (L.); *Rhabdosynochus rhabdosynochus* Mizelle and Blatz, 1941, from *Centropomus undecimalis* (Bloch). All hosts were taken from near the South Jetty at Port Aransas, Texas. The authors are grateful to Dr. Gordon Gunther, former Director, Institute of Marine Science at Port Aransas, Texas for supplying the above host material, and to Dr. John D. Mizelle, Department of Biology, University of Notre Dame, for helpful suggestions and criticisms.

In a recent publication Hargis (1955) described *Rhamnocercus bairdiella* from the marine sciaenid *Baidiella chrysura* (Lacépède). In reviewing this group the author noted that the position of the haptoral bars in the type species, *R. rhamnocercus* Monaco, et al., 1954, was incorrectly reported. The present authors have examined slides of *R. rhamnocercus* from both the original collection of Monaco et al., and paratypes from the U. S. National Museum Helminthological Collection. From these observations it is apparent that the dorso-ventral orientation of the haptor was inaccurately described.

In the same publication Hargis (1955) rejects the subfamily Rhamnocercinae Monaco et al., 1954, on the basis of "(1) dorsal and ventral plaques are probably homologous to the squamodiscs of other diplectanids. (The supposed parenchymatous origin of these and other spinous parts which was mentioned by the original authors is much too uncertain to be a taxonomically reliable character). (2) The detailed similarity of the haptoral bars, anchors, hooks, lateral plaques, body shape and arrangement of internal organs to the same structures in other diplectanids are not counterbalanced by sufficient morphological differences."

We cannot agree with Hargis (1955) on the probable homology of the

haptoral and peduncular structures. It is most inappropriate to speak of homologies when the embryology of the group is virtually unknown. Also, the spine-like hooks of the peduncle and spines of the haptor appear to have their bases deeply rooted in the parenchyma. It is highly improbable that these structures are cuticular (epidermal) as are the superficial squamodiscs on the haptor of the Diplectaninae. Finally, the present authors agree with the original statement of Monaco et al. (1954) that the resemblances between the Diplectaninae and Rhamnocercinae are: "(1) cuticular spines on the body proper; (2) dorsal and ventral pairs of anchors; (3) similar haptoral hooks; and (4) supporting bars associated with anchors. Conspicuous differences are (1) the absence of squamodiscs or cuticular plates on the haptor; (2) the presence of discrete groups or clusters of spines which arise in the parenchyma of the haptor, and whose points project through the surface of this organ; and (3) the presence of rows of spine-like hooks on the peduncles." The subfamily Rhamnocercinae is therefore reinstated on the basis of these observations and the inclusion of the genus *Rhamnocercus* in the Diplectaninae is rejected.

The authors feel that the creation of new terms where older terminology is adequate serves no useful purpose. For example, Hargis' term "plaque" is unacceptable since it does not completely describe the peduncular spine-like hooks and bilateral clumps of haptoral spines characteristic of the subfamily Rhamnocercinae (*See* Webster's unabridged dictionary). Hargis (1955:40) confused the issue on *Rhamnocercus* by stating "that the long, single, longitudinally-furrowed bar is actually dorsal and not ventral" whereas in his emendation of the genus (1955:41) he stated "One ventral and two dorsal bars present." Further this author (1955) is guilty of many gross errors in spelling in regard to which Mayr, Linsley, & Usinger (1953) caution against the failure to read proof against manuscripts.

The emendation of the Diplectaninae by Hargis (1955) is considered premature at this time. Placing the genus *Rhabdosynochus* Mizelle and Blatz, 1941, in the Diplectaninae is rejected pending further study. The minute cuticular spines situated laterally on the peduncle of *Rhabdosynochus* should not be considered structurally similar to squamodiscs on the haptor. The squamodisc has been adequately described and accepted as a diplectanid characteristic. Furthermore, the emendation is incomplete since it makes no reference to the characteristic five bars present in the genus *Lepidotrema* and includes only those forms having: "two pairs of anchors, three or four bars, and 14 hooks . . ."

SUMMARY

The present work describes a new species of Rhamnocercinae from *Micropogon undulatus* (L.). The new species was also recovered from the gills of *Menticirrus littoralis* (Holbrook). It is noteworthy that to date, members of the Rhamnocercinae have been recovered only from the marine Sciaenidae. Three distribution records are listed. The subfamily Rhamnocercinae is reinstated.

REFERENCES

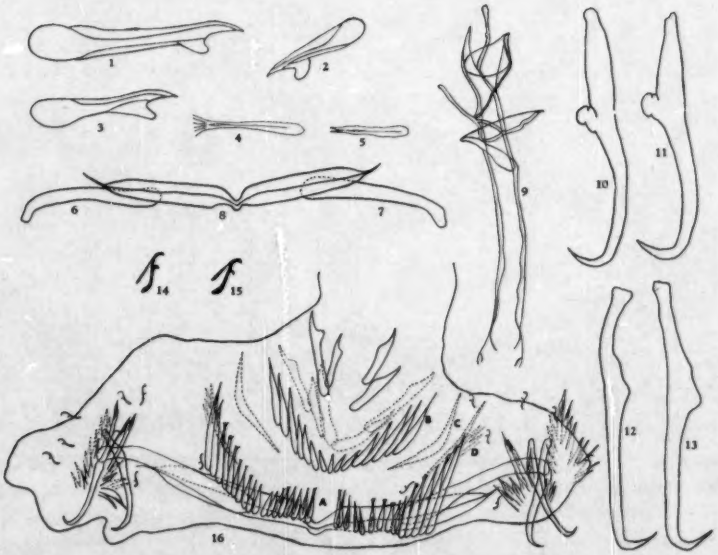
HARGIS, W. J. JR. 1955—Monogenetic trematodes of Gulf of Mexico fishes. Part III. Superfamily Gyrodactyloidea. Quart. J. Fla. Acad. Sci. 18(1):33-47.

MAYR, E., E. GORTON LINSLEY AND R. L. USINGER 1953—Methods and principles of systematic zoology. McGraw-Hill Book Co. Inc.

MIZELLE, J. D. 1936—New species of trematodes from the gills of Illinois fishes. Amer. Midl. Nat. 17(5):785-806.

———1938—Comparative studies on trematodes (Gyrodactyloidea) from the gills of North American freshwater fishes. Ill. Biol. Monogr. 17(1):1-81.

MONACO, L. H., R. A. WOOD, AND J. D. MIZELLE 1954—Studies on monogenetic trematodes. XVI. Rhamnocercinae, a new subfamily of Dactylogyridae. Amer. Midl. Nat. 32(1):129-132.



Figs. 1-16. *Rhamnocercus stichospinus* n. sp.—1-3. Spine-like hooks of peduncle; 4, 5. Individual spines of ventral and/or dorsal row of accessory spines; 6, 7. Dorsal bars; 8. Ventral bar; 9. Circrus; 10, 11. Dorsal anchors; 12, 13. Ventral anchors; 14, 15. Haptoral hooks; 16. Dorsal view of haptor. Figs. 1-5, 9-15, ×395; 6-8, 16, ×183.

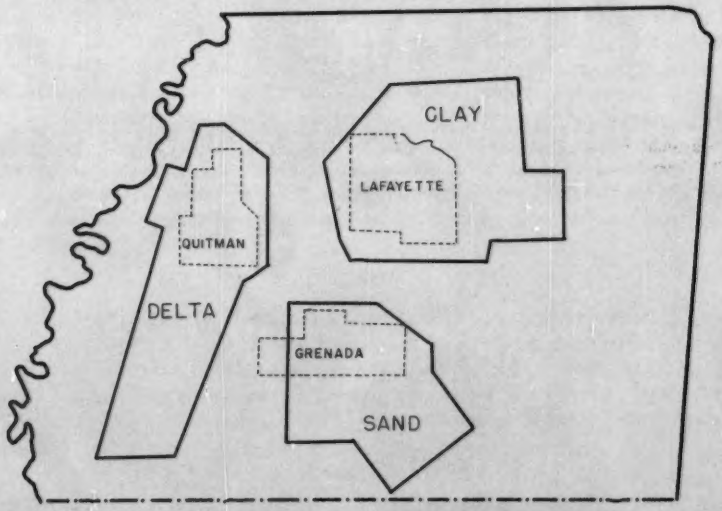
Notes on Fungi from Mississippi
I. Aquatic Phycomycetes

T. W. Johnson, Jr.
Duke University, Durham, North Carolina

There is an obvious paucity of literature on the occurrence and distribution of the aquatic fungi in Mississippi. Judging from the publications of Coker and Matthews (1937) and Sparrow (1943), which treat thoroughly the distribution of the aquatic Phycomycetes, the state is a relatively untouched area of collection. The present contribution is the first of a series of notes on some fungi collected in northern Mississippi during 1952-1954. The writer was particularly interested in the Saprolegniales, hence considerable attention was given to a study of these fungi. Representatives of five other orders of oömycetous fungi were also collected.

In the case of the aquatic fungi at least, records of collection by counties in a limited geographical area are generally of little interest to investigators beyond state boundaries. Therefore, most species listed in this report are located according to soil types in which they were found.

Three principal soil types were selected for the collections. The boundaries within which collecting sites in each of these soils were located are shown on Map 1. The predominant soil type centering around Lafayette County is a shallow topsoil (15-22 cm deep) consisting of a mixture of Memphis silt loam, brown loess, and red clay. Actually, because of severe erosion in this



Map. 1.—Collecting areas (solid line) in northern Mississippi. See text for explanation.

area, a red clay subsoil predominates, and in most collecting sites this is the principal soil. Centering around Quitman County and extending generally southward, is an alluvial soil made up of sandy loam-silty clay loam for a depth of 1/3 - 1 meter. The subsoil in this area is blue clay, but is evident only in deeply eroded streams. Grenada, and adjoining counties to the southeast, have a predominantly sandy loam-clay loam mix for a depth of about 30 cm, with a red clay subsoil intermixed with sand. Contrary to the conditions in the Lafayette County area, erosion is negligible in the Grenada sector, hence the principal soil is sandy loam. In actual practice, it is customary to speak of the Lafayette soil type as clay, the Quitman type as delta soil, and the Grenada sector as sandy soil. With few exceptions, references to sites of occurrence of the species are made according to soil types, and are designated as C, D, or S.

Presently defined species in the aquatic Phycomycetes are, in numerous instances, quite restricted, and allow for little morphological variation. Identification of variants, therefore, may be extremely difficult, particularly in the Saprolegniaceae. It seems advisable that records be made of the aberrant forms so that ultimately species limits may be more firmly fixed and yet be more accurately delimited. For this reason, certain of the taxa are discussed in some detail with respect to the variants which were collected in Mississippi. It is believed that this procedure will to some extent alleviate the taxonomic difficulties which will undoubtedly occur as other collections of these fungi are studied. Citations for the specific binomials are given, but synonyms are not listed. For synonymous taxa, reference is made to Coker and Matthews (1937), and to Sparrow (1943). Species preceded by an asterisk (*) are new records for Mississippi.

The methods of collection and isolation were patterned after those described by Sparrow (1943) and Raper (1937). Isolates were propagated on various types of "bait" (hempseed halves in the case of the Saprolegniaceae, for example), and were incubated in sterile, charcoal-filtered distilled water at 20-23° C. Prior to identification, single spore cultures were made in the case of the filamentous species. Species from submerged fruits and twigs were not isolated, but were identified as they appeared in the pustules.

Fungi Collected

SAPROLEGNIALES

**Saprolegnia delica* Coker, Saprolegniaceae, p. 30. 1923. (C, S). **Saprolegnia diclina* Humphrey, Trans. Amer. Phil. Soc. (N.S.) 17:109. 1893. (C, S). Seven isolates possessed characteristics intermediate between those of the strictest interpretations of these two species. The usual structural features used in the separation of *S. diclina* and *S. delica*, that is, oöspore number, oögonial size, and antheridial branch origin, were not applicable when the isolates were examined on a comparative basis. Whereas some isolates possessed the over-all configuration of sexual organs characteristic of *S. diclina*, sizes of these structures were clearly those representative of *S. delica*. One form isolated from clay soil in Marshall County is not only intermediate between *S. delica* and *S. diclina*, but is also suggestive of *S. crustosa*, a group

species described by Maurizio (1899). Further study may show these three species to be merely variants of a single taxon.

**Saprolegnia ferax* (Gruith.) Thuret, Ann. Sci. Nat. Bot. Sér. III 14:214. 1850. (C, S). **Saprolegnia mixta* deBary, Bot. Zeit. 41:38, 54. 1883. (C, S). These represent a complex of two species with many variants. The fundamental feature of separation seems to be the presence of functional oögonia in discharged zoösporangia in *S. ferax*, and a lack of these in *S. mixta*. Such an oögonial origin is a variable feature, however. Isolates otherwise similar to *S. mixta* produce such oögonia in discharged zoösporangia, while others lack these oögonia but are clearly characteristic of *S. ferax*. Oöspore number is much too variable to be an important diagnostic criterion. As a consequence of the wide variability of the isolates examined, correct identification of each isolate was not possible.

**Saprolegnia monoica* var. *glomerata* Tiesenhausen, Arch. Hydrobiol. 7:277. 1912. (C). The two isolates of this variety (collected from water) are nearest *S. monoica* var. *monoica* with respect to oöspore number. The cultures characteristically produce oögonia having 6-12 oöspores, with 28 as the maximum observed.

**Saprolegnia litoralis* Coker, Saprolegniaceae, p. 54. 1923. (C).

**Saprolegnia kauffmaniana* (?) Pieters, Bot. Gaz. 60:488. 1915. (D). The very large, unpitted oögonia, and large oöspores are the only features which separate this species from *S. ferax*. The single collection from delta soil, however, has sparsely pitted oögonial walls, contrary to Pieters' description of the species. With respect to oögonial and oöspore size, the isolate is nearly identical to *S. kauffmaniana*. It is suggested that Pieters' species may only be a strain of *S. ferax* with larger oöspores and oögonia. If, on further study, *S. kauffmaniana* is shown to be a valid species, however, the present record is the first of this species since its discovery.

Saprolegnia parasitica Coker, Saprolegniaceae, p. 57. 1923. Common on dead fingerlings in ponds and streams throughout the state.

Achlya americana Humphrey, Trans. Amer. Phil. Soc. (N.S.) 17:116. 1893. (C, D). Collected twice. The rarity of this species in Mississippi is contradictory to the writer's distributional records in Michigan where *A. americana* is the most common of the Saprolegniaceae.

**Achlya prolifera* Nees, Nova Acta Acad. Leop.-Carol. 11:514. 1823. (C, D).

**Achlya bisexualis* Coker and A. Couch; Coker, J. Elisha Mitchell Sci. Soc. 42:207. 1927. (C, S).

**Achlya rodrigueziana* F. T. Wolf, Mycologia 33:274. 1941. (C).

**Achlya proliferoides* Coker, Saprolegniaceae, p. 115. 1923. (C, D, S). This species is distinguishable from *A. flagellata* by the coiling antheridial branches which may or may not be functional. All of the nine isolates from Mississippi are characterized by a loss or suppression of the coiling antheridial hyphae during repeated subculturing. *Achlya proliferoides* should perhaps be united with *A. flagellata*, since the single diagnostic characteristic of the former is not stable.

**Achlya spiracaulis* Johnson, Mycologia 41:679. 1949. (C).

**Achlya papillosa* Humphrey, Trans. Amer. Phil. Soc. (N.S.) 17:125. 1893. (C). Figs. 8, 9. The single isolate of this species is a form characterized by sparsely papillate oögonia. Humphrey illustrated the oögonia of *A. papillosa* with densely bullate wall ornamentations.

**Achlya orion* Coker and Couch, J. Elisha Mitchell Sci. Soc. 36:100. 1920. (C, D).

**Achlya apiculata* deBary, Bot. Zeit. 46:635. 1888. (C).

**Achlya recurva* Cornu, Ann. Sci. Nat. Bot. Sér. V, 15:22. 1872. (S). Collected once, from soil, Chickasaw County.

**Achlya megasperma* Humphrey, Trans. Amer. Phil. Soc. (N.S.) 17:118. 1893. (C).

Achlya caroliniana Coker, Bot. Gaz. 50:381. 1910. (C, D). Previously reported from this state by Harvey (1930). One isolate of this species is a variant with abundant antheridial branches and very densely pitted oögonial walls. Nearly all oögonia of this isolate are papillate, and the oöspores average 26 μ in diameter as compared with 22 μ for the type.

**Achlya oblongata* deBary, Bot. Zeit. 46:646. 1888. (C, D).

**Achlya inflata* Coker and Braxton. J. Elisha Mitchell Sci. Soc. 42:211. 1927. (D). Collected once from soil in a cypress stand near Belen, Quitman County.

**Achlya conspicua* Coker, Saprolegniaceae, p. 131. 1923. (C). The single isolate is tentatively identified as this species inasmuch as the oöspheres fail to mature. General configuration of the sexual organs places this species intermediate between *A. flagellata* and *A. americana*.

**Achlya glomerata* Coker, Mycologia 4:325. 1912. (C, D, S).

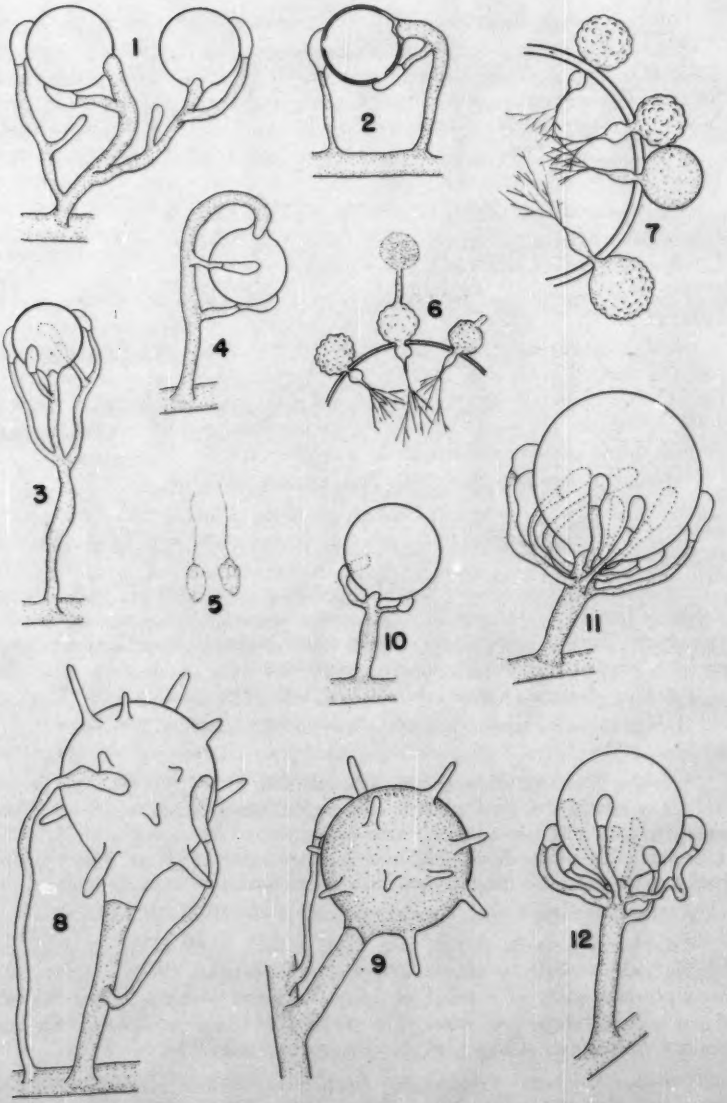
Achlya diffusa Harvey. J. Elisha Mitchell Sci. Soc. 58:29. 1942. (C, D. S).

**Achlya klebsiana* Pieters, Bot. Gaz. 60:486. 1915. (C, D, S). Several isolates possessed the small number of oöspores characteristic of *A. michiganensis* (Johnson, 1950), a species now considered to be merely a strain of *A. klebsiana*. An isolate from delta soil is characterized by very long oögonial stalks, these being 4-8 times longer than the diameter of the oögonium.

Achlya flagellata Coker, Saprolegniaceae, p 116. 1923. (C, D, S).

**Achlya oligacantha* deBary, Bot.. Zeit. 46:647. 1888. (D). A single collection, characterized by centric oöspores. Observations on this isolate confirms previous study of a collection from Maryland which also (rarely) produced mature, centric oöspores. The position of *A. oligacantha* in the subgenus *Centroachlya* (Coker, 1923) seems firmly established.

**Achlya colorata* Pringsheim, Sitzungsber. Akad. Berlin 1882:889. 1882. (C, D). Two variants of this species were collected, and are briefly described. Isolate 584: oögonial stalks generally 4-6 times longer than the diameter of the oögonium; other characteristics as defined by Coker and Matthews. Isolate 558: oöspores predominantly 30-34 μ in diameter, 1-3 in number; other features as described by Coker and Matthews.



Figs. 1-12.—1-4. Oögonia and antheridia of *Dictyuchus pseudoachlyoides* (X390); 5-7. *Rhizidiomyces apophysatus*. 5. Zoöspores (X935); 6. Sporangia, one showing spore discharge (X390); 7. Sporangia (X870); 8, 9. Oögonial wall ornamentations of *Achlya papillosa* (X390); 10-12. *Achlya racemosa*. 10. Oögonium and antheridial branches characteristic of the species (X390); 11, 12. Oögonia and antheridia of forma *maxima* (X390).

**Achlya racemosa* Hildebrand, Jahrb. wiss. Bot. 6:249. 1867. (C, D). Figs. 10-12. Three of the 16 collections of this species represent von Minden's *A. racemosa* var. *stelligera* forma *maxima* (1912). These isolates are characterized by large oögonia and profuse androgynous antheridial branches (figs. 11, 12), features which apparently led von Minden to describe forma *maxima*. Abundant antheridial branches of the Mississippi isolates, however, are produced only when colonies are propagated on hempseed. Propagation on cornmeal agar block, grubs, or on flies, result in suppression of antheridial branches. Oögonia produced by colonies on hempseed are much larger than those characteristic of *A. racemosa* (see figs. 10, 11). It appears that nutrition has some influence on the morphology of these isolates, since they can be changed by proper selection of substratum to either *A. racemosa* or forma *maxima* of the species.

**Aphanomyces stellatus* deBary, Jahrb. wiss. Bot. 2:178. 1859. (D, S).

**Isoachlya unispora* Coker and Couch; Coker, Saprolegniaceae, p. 87. 1923. (C, S). Particularly abundant in the soil bordering Sardis Reservoir, Panola County.

**Isoachlya intermedia* (Coker and Harvey) Coker; Coker and Matthews, North Amer. Flora 2(1):27. 1937. (C. D).

Isoachlya subterranea Dissmann, Beih. Bot. Cent. 58:110. 1931. (C, D, S). *Isoachlya itoana* (Nagai, 1931) and *I. glomerata* (Richter, 1937) are synonymous with *I. subterranea*.

**Isoachlya toruloides* Kauffman and Coker; Kauffman, Amer. J. Bot. 8:231. 1921. (C). One isolate of this species possesses the catenulate oögonia of *I. monilifera*, but has no functional antheridia which places it nearer *I. toruloides*. In other collections the antheridial branches may or may not be formed. Size of oögonia and oöspores in the Mississippi collections are rather intermediate between those recorded for *I. toruloides* and *I. monilifera*. For the present, the isolates are considered variants of *I. toruloides* with the reservation that on further examination of other collections, the distinctions between these two species may no longer be tenable.

Dictyuchus monosporus Leitgeb, Jahrb. wiss. Bot. 7:357. 1869. (C, D, S).

**Dictyuchus anomalus* Nagai, Jour. Fac. Agr. Hokkaido Imp. Univ. 32:28. 1931. (C, D, S). The presence of true-net zoösporangia in this species is the only characteristic separating it from *D. missouriensis*. Should this feature prove to be variable, as shown for *D. pseudodictyon* (Johnson, 1951; Johnson, *et al*, 1951), the two species should be united.

**Dictyuchus missouriensis* Couch, J. Elisha Mitchell Sci. Soc. 46:227. 1931. (D). Distinguishable from the foregoing species only by the false-net zoösporangia.

**Dictyuchus pseudoachlyoides* Beneke, J. Elisha Mitchell Sci. Soc. 64:263. 1948. (D). Figs. 1-4. The single isolate of this species varied somewhat from the type. The oögonial walls are generally pitted under the point of attachment of the antheridial cells (occasionally elsewhere), and the oögonia are predominantly larger (37-42 μ) than described for the type. Antheridial branch origin is variable in the Mississippi isolate, with monoclinous origin

appearing as frequently as androgynous. Beneke described his species as having predominantly androgynous branches. Furthermore, the isolate generally produces pendant oögonia (figs.2, 4) suggestive of the oögonia of *Achlya orion*.

**Thraustotheca primoachlya* Coker and Couch, J. Elisha Mitchell Sci. Soc. 40:198. 1924. (S). A single collection from soil near Duck Hill, Montgomery County.

Geolegnia inflata Coker and Harvey; Harvey, J. Elisha Mitchell Sci. Soc. 41:154. 1925. (C). Collected from soil at a single station along the shore line, Spring Lake, Marshall County. Previously reported from Mississippi by Harvey (1930).

Geolegnia septisporangia Coker and Harvey; Harvey, J. Elisha Mitchell Sci. Soc. 41:155. 1925. (C). Collected from soil at two stations: Coles Point, Sardis Reservoir, Panola County, and the east bank of the Tombigbee River near Fulton, Itawamba County. Also reported by Harvey (1930).

**Brevilegnia diclina* Harvey, J. Elisha Mitchell Sci. Soc. 42:243. 1927. (D).

**Brevilegnia subclavata* Couch, J. Elisha Mitchell Sci. Soc. 42:229. 1927. (D).

**Brevilegnia linearis* Coker and Braxton; Coker, J. Elisha Mitchell Sci. Soc. 42:214. 1927. (D).

**Brevilegnia unisperma* var. *delica* Coker and Alexander; J. Elisha Mitchell Sci. Soc. 42:214. 1927. (D). Eight collections of this variety were obtained. While the general characteristics of the isolates were quite similar to those of the variety *delica*, the preponderance of dictyoid zoösporangia was common to all. Coker mentioned the presence of dictyoid zoösporangia in *B. unisperma* var. *delica*, but apparently his isolate produced these only rarely. In the Mississippi collections the majority of the zoösporangia are dictyoid, with only a very few (in older colonies) having the *Brevilegnia* type of spore discharge. Brevilegnoid zoösporangia are found, rarely, in some strains of *Dictyuchus anomalus*, and if this should be found to be characteristic of other species of *Dictyuchus*, transfer of *B. unisperma* var. *delica* is indicated and warranted. Such a transfer would, in effect, preserve the generic limits of *Brevilegnia*. With respect to type of oögonia, *B. unisperma* var. *delica* has little in common with B. *unisperma* var. *unisperma*. Papillate or tuberculate oögonia are lacking in the variety *delica*, but are produced by the varieties *unisperma*, *montana*, and *litoralis*.

**Leptolegnia eccentrica* Coker and Matthews; Coker, J. Elisha Mitchell Sci. Soc. 42:215. 1927. (D, S). Collected twice. *Leptolegnia subterranea* was reported from Mississippi by Harvey (1930).

**Pythiopsis cymosa* deBary, Bot. Zeit. 46:631. 1888. (C).

BLASTOCLADIALES

**Blastocladia pringsheimii* Reinsch, Jahrb. wiss. Bot. 11:298. 1878. On apples, and on submerged fruits of *Melia azederach*, collected from Taylor Lake, Lafayette County, and Spring Lake, Marshall County. The habit of

this fungus is quite variable, particularly on chinaberry fruits. A number of pustules on this substratum contained plants very similar to *B. gracilis* Kanouse (1927), but which were also easily recognizable as *B. pringsheimii*. Miss Kanouse's species might well be united with *B. pringsheimii*, but this procedure should await data from single spore cultural studies of the variability of the latter.

**Blastocladia ramosa* Thaxter, Bot. Goz. 21:50. 1896. On submerged twigs of *Carya aquatica*, Cat Hair Creek, Lafayette County.

Allomyces arbuscula E. J. Butler, Ann. Bot. London 25:1027. 1911. (C, D, S). Very common, particularly in dry soil along the edge of Enid and Sardis reservoirs, and in delta soils in cultivated fields.

**Allomyces moniliformis* Coker and Braxton, J. Elisha Mitchell Sci. Soc. 42:139. 1926. (D, S).

MONOBLEPHARIDALES

**Monoblepharis polymorpha* Cornu, Bull. Soc. Bot. France 18:59. 1871. Collected twice on submerged twigs in a small, spring-fed pond, Tallahatchie Experimental Forest, Lafayette County.

Monoblepharella endogena Sparrow, Mycologia 45:593. 1953. (D). A single collection from soil taken along the bank of an intermittent stream one mile west of Darling, Quitman County. Sparrow described this fungus as a new species isolated from (delta) soil near Clarksdale.

**Gonopodya polymorpha* Thaxter, Bot. Gaz. 20:481. 1895. Collected twice from submerged twigs of *Taxodium distichum* var. *nutans* in Spring Lake, Marshall County, and once on a similar substratum, Hurricane Creek, Lafayette County.

LEPTOMITALES

Leptomitus lacteus (Roth) Agardh, Systema Algarum, p. 47. 1824. (C). Common in diluted sewage effluent in streams.

**Mindeniella spinospora* Kanouse, Amer. J. Bot. 14: 301. 1927. Collected three times on apples placed in pools along Toby Tubby Creek, Lafayette County.

**Rhipidium americanum* Thaxter, Bot. Gaz. 21:327. 1896.

CHYTRIDIALES

**Rhizophydium carpophilum* (Zopf) Fischer, Rabenhorst Kryptogamen-Fl. 1(4):95. 1892. Parasitic on oögonia of *Isoachlya unispora*, an unreported host for this species of *Rhizophydium*.

**Rozella achlyae* Shanor, J. Elisha Mitchell Sci. Soc. 58:100. Collected once as a parasite of *Dictyuchus anomalus*.

LAGENIDIALES

**Olpidiopsis saprolegniae* var. *saprolegniae* (Braun) Cornu, Ann. Sci. Nat. Bot. Sér. V, 15:145. 1872.

**Olpidiopsis saprolegniae* var. *levis* Coker, Saprolegniaceae, p. 185. 1923. Parasitic on *Saprolegnia ferax* (?) and *S. delica* (?).

**Olpidiopsis fusiformis* Cornu, Ann. Sci. Nat. Bot. Sér. V, 15:147. 1872. Observed in two collections of *Achlya flagellata*. The morphological characteristics of the Mississippi collections suggest that *O. achlyae* (McLarty, 1941) is the same as *O. fusiformis*. Our collections can be referred with equal confidence to either species. Further study, particularly of the host ranges, may make such a change advisable.

**Olpidiopsis* sp. A new species, parasitic in *Achlya glomerata*. The species is described elsewhere (Johnson, 1955).

HYPHOCHYTRIACEAE

**Rhizidiomyces apophysatus* Zopf, Nova Acta Acad. Leop.-Carol. 47:188. 1884. Figs. 5-7. Found once as a parasite of *Achlya flagellata* collected from soil in a roadside ditch, one mile north of Sweatman, Montgomery County. The single collection seems to be a well-marked variant of Zop's species, and is worthy of a brief description:

Zoösporangia spherical, subspherical, or pyriform; 18-51 μ in diameter; wall colorless, stout, smooth, roughened, irregular, or slightly bullate; discharge tube apical, straight or irregular. Subsporangial apophysis spherical, turbinate, or pyriform; 11- 21 μ in diameter. Rhizoids freely branched, arising from 1-3 main axes from base of the apophysis. Zoöspores ovoid to slightly irregular; 3-7 μ long, with a single refractive globule; anteriorly uniflagellate. Parasitic on oögonia of *Achlya flagellata*.

The presence of roughened, bullate, or slightly irregular sporangial walls in addition to the smooth-walled sporangia, mark our collection as a distinct form of Zopf's speices. *Rhizidiomyces apophysatus* has predominantly smooth-walled zoösporangia, but occasionally may produce echinulate ones. Although spiny sporangial walls were not observed in the Mississippi collection, bullate or verrucose walls were common. With respect to other characteristics such as flagellation, and size of zoöspores and zoösporangia, there is little doubt that the parasite on *Achlya flagellata* is merely a variant of *R. apophysatus*. Zopf's species seems to be rather variable with respect to sporangial wall configuration.

Acknowledgments.—I am indebted to Miss Jacqueline Surratt for assistance in the collection and isolation of these fungi. Special thanks are accorded the University of Mississippi and the Board of Trustees of State Institutions of Higher Learning for funds to defray costs involved in this study.

SUMMARY

Sixty-four species of aquatic Phycomycetes are reported from Mississippi. Of these, 54 species are recorded for the first time from this state.

REFERENCES

COKER, W. C. 1923—The Saprolegniaceae, with notes on other water molds. Univ. North Carolina Press, Chapel Hill.

——— AND V. D. MATTHEWS 1937—Blastocladiales, Monoblepharidales, Saprolegniales. North Amer. Flora 2(1):1-76.

HARVEY, J. V. 1930—A taxonomic and morphological study of some members of the Saprolegniaceae. J. Elisha Mitchell Sci. Soc. 45:319-332.

HUMPHREY, J. E. 1893—The Saprolegniaceae of the United States, with notes on other species. Trans. Amer. Phil. Soc. (N.S.) 17:63-148.

JOHNSON, T. W., JR. 1950—A new *Achlya* from Mackinac Island, Michigan, with notes on other species. Mycologia 42:391-402.

——— 1951—An isolate of *Dictyuchus* connecting the false-net and true-net species. Ibid. 43:367-372.

——— 1955—A species of *Olpidiopsis* parasitic in *Achlya glomerata*. J. Elisha Mitchell Sci. Soc. (In press).

———, A. W. ZEIGLER, AND BETTY LINTHICUM 1951—A note on *Dictyuchus pseudodictyon*. Mycologia 43:728-729.

KANOUSE, BESSIE *B.* 1927—A monographic study of special groups of the water molds. I. Blastocladiaceae. Amer. J. Bot. 14:287-306.

MCLARTY, D. A. 1941—Studies in the family Woroninaceae—I. Discussion of a new species including a consideration of the genera *Pseudolpidium* and *Olpidiopsis*. Bull. Torrey Bot. Club 68:49-66.

MAURIZIO, A. 1899—Beiträge zur Biologie der Saprolegnieen. Mittheil. Deutsch. Fischerei-Vereins 7:1-66.

MINDEN, M. VON 1912—Phycomycetes. IV. Reihe: Saprolegniineae. Kryptogamenfl. Mark Brandenburg 5:479-606.

NAGAI, M. 1931—Studies on the Japanese Saprolegniaceae. J. Fac. Agr. Hokkaido Imp. Univ. 32:1-43.

RAPER, J. R. 1937—A method of freeing fungi from bacterial contamination. Science 85:342.

RICHTER, W. 1937—Vorarbeiten zu einer Saprolegniaceen-flora von Marburg. Flora (N.S.) 131:227-262.

SPARROW, F. K. 1943—Aquatic Phycomycetes, exclusive of the Saprolegniaceae and *Pythium*. Univ. Michigan Press, Ann Arbor.

——— 1953—A new species of *Monoblepharella*. Mycologia 45:592-595.

Florida Scytonemataceae I.[1]

C. S. Nielsen and Grace C. Madsen
Florida State University, Tallahassee

Collections containing species of Scytonemataceae from Florida were first made by Captain John Donnell Smith in March of 1878 and by H. W. Ravenel a few years later (Wolle, 1887). These early specimens have more recently been re-examined by Drouet (1939) and will be mentioned subsequently. The few collections by R. Thaxter from south Florida in 1897 and by Marshall A. Howe in 1902 from the St. Augustine area are indicated. Later records are the more scattered reports of various visitors to the state. In 1942 more systematic collecting was undertaken by M. A. Brannon in the Gainesville area and in 1948 in the Tallahassee area by various members of the Botany staff of Florida State University.

The assistance of Dr. Drouet for the determination of the specimens is most gratefully acknowledged. For the preparation of the illustrations the authors are indebted to Miss Sylvia A. Earle. Herbaria in which the cited specimens are located are designated as follows: C—Chicago Natural History Museum; D—personal herbarium of Francis Drouet; F—Florida State University; H—Farlow herbarium of Harvard University; N—United States National herbarium; P—University of Pennsylvania; U—University of Florida; W—Shallert's herbarium at Winston-Salem, N. C. and Y—New York Botanical Garden. References to Bornet and Flahault are to their "Revision des Nostocacées hétérocystées contenues dans les principaux herbiers de France" (1886-88) unless otherwise indicated.

Key to the Genera of the Scytonemataceae

A. More than one trichome within sheath ..... B
  B. Filaments subdichotomously branched; heterocysts basal; freshwater plants. No record of Florida collections ..... *Desmonema*
  BB. Filaments pseudo-branched, solitary or geminate; branches forming between heterocysts; plants terrestrial. No record of Florida collections ..... *Diplocolon*[2]
AA. Trichome solitary within sheath C
  C. Filaments simple ..... D
    D. Filaments up to 10μ wide ..... *Fremyella*
    DD. Filaments up to 17μ wide ..... *Aulosira*
  CC. Filaments Pseudo-branched ..... E
    E. Pseudo-branches solitary, forming below heterocysts, rarely midway between heterocysts and geminate ..... F

---

[1] Contribution Number 64, Botanical Laboratory, Florida State University.

[2] *Scytonema Heppii* (Naeg.) Wolle was reported for the state by Wolle (1887) (Florida, *Smith*, Mar. 1878). This species is a synonym of *Diplocolon Heppii* B. & F. (Drouet 1939). The species has also been reported for Florida by Tilden (1910); the *Smith* 1878 collection has been referred to *Scytonema crustaceum* B. & F. by Drouet (1939).

FF. Filaments flexuous; plants aquatic ..... *Tolypothrix*
EE. Pseudo-branches geminate, forming midway between heterocysts, rarely below heterocysts ..... *Scytonema*

FF. Filaments fragile; plants terrestrial ..... *Hassallia*

FREMYELLA J. DeToni

A. Fresh water plants; both basal and intercalary heterocysts produced simultaneously.
B. Filaments stellate, 6-7μ; sheath simple, thin, firm ..... 1. *F. tenera*
BB. Filaments sparse, up to 10μ wide; sheath full, double; inner membranaceous, thin, outer mucous, wide ..... 2. *F. diplosiphon*
AA. Plants marine; heterocysts basal.
C. Densely caespitose; filaments straight, 6-7μ wide, bases bulbously thickened; cells considerably shorter than wide ..... 3. *F. grisea*
CC. Filaments 5.5-6.5μ wide; cells quadrate-subquadrate ..... 4. *F. longifila*

1. FREMYELLA TENERA (Born. & Flah.) J. DeToni. Noter. Nomencl. Algol. VIII. 1936

Fig. 1

Filaments 1 mm long, 6-7μ wide, curved at base, slightly flexuous; sheath thin, firm, uniform, hyaline; trichomes 5μ wide, blue-green; lower cells twice as long as diameter, upper quadrate; basal heterocysts oblong, intercalary cylindrical.

Specimens seen were found with *Anabaena variabilis* B. & F. and *Phormidium autumnale* Gom. The species was reported for the state by Brannon (1952).

ALACHUA CO.: in Hatchett creek, Gainesville, *Brannon* 66, 8 June 1942 (C); 141, Feb. 1943 (C, U); 189, 29 July 1943 (C).

2. FREMYELLA DIPLOSIPHON (Born. & Flah.) Drouet. Field Mus. Bot. Ser. 20(2):32. 1939

Fig. 2

Cells 4.5 to 6μ wide, lower contracted at cross-walls, longer than diameter, upper less contracted, equal to or shorter than diameter; sheath double, colorless; the outer irregular, mucous, often measuring double the diameter of the trichome, up to 10μ wide; inner thin, 4.7-6.7μ wide, membranaceous, precisely cylindrical, firm; basal heterocysts depressed or spherical, intercalary heterocysts more or less elongate; spores seriate, cylindrical, equal in width to vegetative cells, up to ¼ longer than diameter.

Specimens have been found with young *Stigeoclonium* spp., sterile *Oedogonium* spp. and *Plectonema Nostocorum* Gom. The species has been reported for the state by Brannon (1945, 1952) and Nielsen & Madsen (1948b).

ALACHUA CO.: in Hatchett creek, Gainesville, *Brannon* 2, 22, 34, 174, 178, Feb. 1942 (C, U); *Brannon* 1947 (C); 164, 11 Apr. 1943 (C). LEON CO.: Fla. State Univ. Greenhouse, *Nielsen* 200, July 1948 (F).

3. FREMYELLA GRISEA (Born. & Flah.) J. DeToni. Noter. Nomencl. Algol. VIII. 1936

Fig. 3

Stratum caespitose, tomentose, orbicular, dark green, turning violet when dry; filaments 1 mm long, 6-7μ wide, bulbous and curved at base, later straight and densely crowded; sheath thin, firm, continuous, hyaline; trichomes 5-6μ wide, dark olive-green; cells from ½ to 3 times shorter than diameter; heterocysts basal and hemispherical.

Specimens seen have been found with *Anacystis* spp. and *Calothrix con-*

fervicola B. & F. It has been reported for the state by Madsen & Nielsen (1950).

FRANKLIN CO.: on scallop shell, 3½ miles ESE of St. Mark's lighthouse, *H. J. Humm*, June 26, 1952 (C). PINELLAS CO.: Piney Pt., Tampa bay, *H. J. Humm* 1, Apr. 2, 1956 (C). WAKULLA CO.: in pilings in St. Mark's river, Port Leon, *Drouet & E. M. Atwood* 11458a, Jan. 26, 1949 (C, F).

4. FREMYELLA LONGIFILA (W. R. Taylor) Drouet. Field Mus. Bot. Ser. 20(6):130. 1942

Filaments epiphytic, much elongated; trichomes slender, very slightly constricted at cross-walls, diameter 5.6-6.5μ; cells as long as broad or somewhat shorter; sheaths thin, colorless; pigment blue-green or pinkish; heterocysts basal, spherical to oval, 9-10μ in diameter, or intercalary, oval to cylindrical, 5.6-6.5μ in diameter, 11-12μ long.

The species has been reported for the state by W. R. Taylor (1928).

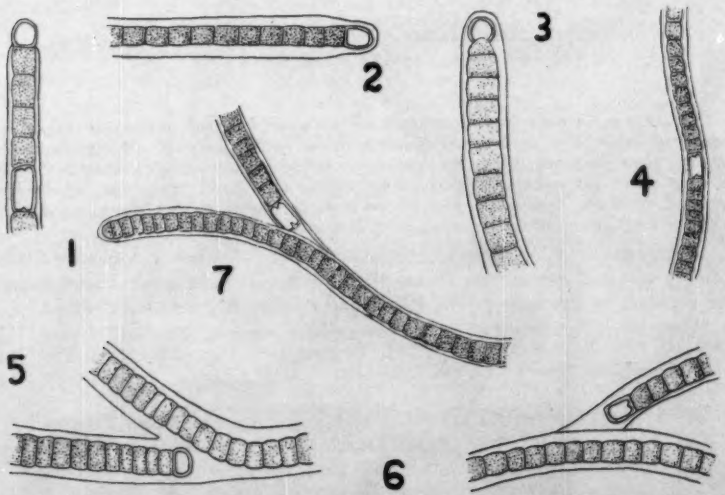
MONROE CO.: on *Cladophora* and *Chaetomorpha*, at moat, Garden Key, Dry Tortugas, *Taylor* 134, June 22, 1924 (C).

AULOSIRA Kirchner

AULOSIRA IMPLEXA Bornet & Flahault

Fig. 4

Filaments 5-10 mm long, straight, fasciculate, 7-17μ (commonly 12μ) wide; sheath thin, hyaline; trichomes 8-9μ wide; cells in vegetative filaments quadrate to ½ diameter, in reproductive twice as long as wide, slightly constricted at cross-walls, granular; heterocysts yellowish, quadrate to oblong; spores 4-32 in series, 6-9μ wide, 16-34μ long, outer wall smooth.



Figs. 1-7.—1. *Fremyella tenera* (Born. & Flah.) J. De Toni ×640; 2. *Fremyella diplosiphon* (Born. & Flah.) Drouet ×560; 3. *Fremyella grisea* (Born. & Flah.) J. DeToni ×720; 4. *Aulosira implexa* Born & Flah. ×300; 5. *Hassallia byssoidea* Born. & Flah. ×400; 6. *Tolypothrix lanata* Born. & Flah. ×280; 7. *Tolypothrix tenuis* Born. & Flah. ×320.

Some of the specimens cited below were found with *Hapalosiphon pumilus* B. & F. The species has been reported for the state by Brannon (1945, 1952) and Crowson (1950).

LAKE OKEECHOBEE: on floating *Eleocharis, J. E. Davis, Jr.* 16, 17, 279, Oct. 10, 1941 (C, U). ALACHUA CO.: in Sink II, Hibiscus Pk., Gainesville, *Brannon* 112, Oct., 1942 (C, U); *Brannon* 82, July 27, 1942 (C, U); *Brannon* 285, Aug. 21, 1944 (C). DADE CO.: Cocoanut Grove, *R. Thaxter,* 1897 (C). LEE CO.: dried pool, region of Hendry Creek, about 10 miles south of Fort Myers, *Paul C. Standley* 73229, March 11-25, 1940 (C). OSCEOLA CO.: in ditch, 2 miles west of Kissimmee on Vineland rd., *A. H. Johnston* 1936-1938, Aug. 30, 1949 (C, F). WAKULLA CO.: "T-pond" at Phillip's Pool, St. Mark's Wildlife Refuge, *Nielsen, Madsen & Crowson* 650, Oct. 7, 1948 (C, F).

HASSALLIA Berkeley

HASSALLIA BYSSOIDEA Bornet & Flahault

Fig. 5

Stratum pulvinate-tomentose, becoming dark, black; filaments 1 mm tall, 10-15μ wide, irregularly pseudo-branched; pseudo-branches short erect-extended; sheath firm, slender, gold to dark, very fragile, tubular, continuous, occasionally subocreate; trichomes 9-11μ wide, torulose, olive-colored; cell length shorter by 1/3 to 1/2 diameter; basal heterocyst 1, rarely 2.

The cited specimens were found with *Gloeocapsa alpicola* (Lyngb.) Bornet, *G. atrata* (Breb.) Kütz., *Mesotaenium macrococcum* (Kütz.) Roy and *Trentepohlia aurea* (L.) Martius. The species was reported for the state by Nielsen & Madsen (1948b) and Brannon (1952).

ALACHUA CO.: Hibiscus Pk., Gainesville, *Brannon* 229, May, 1944 (C, U); Science Hall, Univ. Fla. campus, Gainesville, *Brannon* 263, Aug., 1944 (C, U); 304, Aug. 24, 1945 (C). JEFFERSON CO.: near Lamont, *Paul C. Standley* 92757, Mar. 6, 1946 (C). LAKE CO.: greenhouse wall, Exp. Sta., Leesburg, *Brannon* 250, July, 1944 (C, U). LEE CO.: tree trunk, region of Hendry Creek, about 10 miles south of Fort Myers, *Paul C. Standley* 73239, 73360, 73450, Mar. 11-25, 1940 (C). LEON CO.: Crane lake at Meridian rd., *Nielsen, Madsen & Crowson* 201, July, 1948 (C, F); Judge Andru's magnolia forest, Lake Iamonia, *Nielsen & Madsen* 385, 392, Aug., 1948 (C, F). LEVY CO.: Otter creek, *Brannon* 237, June 2, 1944 (C). MANATEE CO.: on stone wall of church, Bradenton, *C. B. Stifler,* Feb., 1943 (C). MARION CO.: on tree, Silver Springs, *Drouet & Brannon* 11022, Jan. 19, 1949 (C). ORANGE CO.: Orlando, *Paul C. Standley* 92643, 92645, Mar. 17, 1946 (C). PALM BEACH CO.: on scrub oak, West Palm Beach, *R. Thaxter,* Dec., 1897 (C); on trunks of trees along Pine Way, east of County Rd., Palm Beach, *Drouet & Louderback* 10214, Dec. 24, 1948 (C). VOLUSIA CF.: Daytona, *R. Thaxter,* 1898-99 (C). WAKULLA CO.: St. Mark's River, Little Natural Bridge, *Nielsen & Madsen* 550, Oct. 30, 1948 (C, F).

TOLYPOTHRIX Kützing

A. Trichomes 10μ wide, heterocysts 1-4 ..... *T. lanata*
AA. Trichomes 6-8μ wide, heterocysts 1-5 ..... *T. tenuis*

TOLYPOTHRIX LANATA Bornet & Flahault

Fig. 6

Specimens were found with *Cosmarium* spp. *Desmidium Swartzii* Ag., *Hapalosiphon pumilus* B. & F., *Mougeotia* spp. and *Oedogonium* spp. The species has been reported for the state by Nielsen & Madsen (1948a) and Crowson (1950).

LEON CO.: Six-mile pond, Apalachicola Nat'l. Forest, on U. S. Highway 319, *Nielsen,*

Madsen & Crowson 604-610, Oct. 30, 1948 (C, F); Crane lake, 9 miles north of Tallahassee on Meridian Rd., *Nielsen & Madsen* 629, Oct. 31, 1948 (C, F); west shore of Six-mile Pond, U. S. Highway 319, Apalachicola Nat'l. Forest, *Drouet, Crowson & Thornton* 11404, Jan. 25, 1949 (C, F). WAKULLA CO.: Spillway Dam, Phillip's Pool, St. Mark's Wildlife Refuge, *Nielsen, Madsen & Crowson* 503, Oct. 9, 1948 (C, F); 725, Dec. 5, 1948 (C, F); *Drouet, Madsen & Crowson* 826, Jan. 14, 1949 (C, F); "T-pond," part of Lake Phillips, St. Mark's Wildlife Refuge, ¼ mile E. of Port Leon, *Drouet, Madsen & Crowson* 10835, 10841, Jan. 13, 1949 (C, F).

TOLYPOTHRIX TENUIS Bornet & Flahault

Fig. 7

Specimens were found with *Cladophora* spp., *Lyngbya versicolor* Gom., *Microcoleus* spp., *Schizothrix Lamyi* Gom., *Scytonema figuratum*, B. & F. and *Spirogyra* spp. Nielsen & Madsen (1948b) and Brannon (1952) have reported the species for the state.

ALACHUA CO.: Hibiscus pk., Gainesville, *Brannon* 357, July 8, 1946 (C, U); 366, 367, Sept. 4, 1946 (C); 604, Apr., 1948 (C, U); June 1, 1949 (C, U). BAY CO.: shore of west arm of St. Andrew's Bay, West Bay, *Drouet & Nielsen* 10871a, Jan. 15, 1949 (C, F). ESCAMBIA CO.: fresh water pool behind dunes, Gulf Beach, *Drouet, Nielsen, Madsen & Crowson* 10530, 10539, 10541, 10547, Jan. 8, 1949 (C, F). LEON CO.: shallow water of cypress swamp, State Highway 61, N. of Leon-Wakulla county-line, *Drouet, Madsen & Crowson* 11541, Jan. 27, 1949 (C, F). MANATEE CO.: on *Chara* sp. in a fresh water lake, Manatee, *Cloyd B. Stifler*, Jan. 6, 1943 (C). WAKULLA CO.: Mounds pool, roadside ditch, St. Mark's Wildlife Refuge, *Nielsen, Madsen & Crowson* 122, 123, 126, June, 1948 (C, F); small sulphur spring, ½ mile N. of Newport, *Drouet, Crowson & Thornton* 11362, 11366, Jan. 25, 1949 (C, F); Spillway Dam, Phillip's Lake, St. Mark's Wildlife Refuge, *Nielsen & Crowson* 921, 922, 927, Feb. 15, 1949 (C, F).

Tolypothrix Ravenelii Wolle has been reported for Florida by Tilden (1910). The specimen was collected by Ravenel on sandstone rock, Gainesville, Dec. 1877. Drouet (1939) states that he has been unable to find the Florida specimen in the Wolle herbarium and therefore has included it in the list of species inquirenda.

REFERENCES

BORNET, ED., AND CH. FLAHAULT 1868-88—Revision des Nostocacées Hétérocystées Continues dans les Principaux Herbiers de France. Ann. Sci. nat., VII[e] Sér., Bot. III, IV, V, and VII.

BRANNON, MELVIN A. 1945—Factors affecting the growth of Myxophyceae in Florida. Quart. J. Fla. Acad. Sci. 8(4):296-303.

——— 1952—Some Myxophyceae in Florida. Ibid. 15(2):70-78.

CROWSON, DOROTHY E. 1950—The algae of a modified brackish pool. Fla. State Univ. Studies 1:1-32.

DROUET, FRANCIS 1939—Francis Wolle's filamentous Myxophyceae. Field Mus. Nat. Hist. Bot. Series 20(2):17-64.

MADSEN, GRACE C. AND C. S. NIELSEN 1950—Check list of the algae of northern Florida II. Quart. J. Fla. Acad. Sci. 15(1-4): 3-21.

NIELSEN, C. S., AND GRACE C. MADSEN 1948a—Preliminary check list of the algae of the Tallahassee area. Ibid. 11(2-3):63-66.

——— 1948b—Check list of the algae of northern Florida I. Ibid. 11(4):111-117.

TAYLOR, WILLIAM R. 1928—Marine algae of Florida with special reference to the Dry Tortugas. Papers from the Tortugas Laboratory (Carnegie Institution of Washington) 25:1-219.

TILDEN, JOSEPHINE 1910—Minnesota Algae, Vol. I, Bot. ser. VIII, Minneapolis, Minn.

WOLLE, FRANCIS 1877—Fresh Water Algae of the United States. Bethlehem, Pa.

Taxonomy of American Atriplex

Grant Dukelow Brown
Pomona College, Claremont, California

Historical Review

On the first day of autumn in the year 1804, Captain Meriwether Lewis of the Lewis and Clark Expedition, collected a plant specimen at the "Big Bend of the Missouri." This specimen was described later by Pursh (1814) as being a new species of the genus *Calligonum* L. in the Polygonaceae. Subsequently, Nuttall (1818) placed it in the Chenopodiaceae as a member of the genus *Atriplex* L. Thus began the discovery and describing of shrubby atriplices native to the United States.

In *Species Plantarum* Linnaeus (1753) limited the concept of the genus *Atriplex* drastically by placing most of the species attributed to it by many of the early eighteenth century botanists into other genera of the Chenopodiaceae. The first post-Linnaean generic division of *Atriplex* was that of *Obione*, as proposed by Gaertner (1791). The constant character of the inverted ovule, described from the single species *O. muricata*, was the basis for the division. In the United States it was accepted by Torrey as a valid proposal, and he described half of the species treated in this paper as members of the genus *Obione*. Watson (1871) favored Torrey's system in describing the species *torreyi*, but in 1874 he reduced *Obione* into synonymy under *Atriplex*. Hall (1923) gave *Obione* subspecific rank under *Atriplex*. A few European botanists, e. g. Moquin-Tandon (1840), Ascherson and Graebner (1913), and Ulbrich (1934), have retained *Obione* as a genus.

Pterochiton was the next generic proposal to be advanced. Torrey and Fremont (1845) based its exclusiveness upon the longitudinally winged bract character of *Atriplex canescens*. Nuttall (1848) recognized the division, but otherwise *Pterochiton* has been considered as nothing more than a section or subgenus of *Atriplex*.

Other generic divisions of the genus not directly related to the group treated in this paper have been reduced to synonymy under *Atriplex* by Standley (1916), and no attempt has been made by the author to substantiate or refute his treatment. The reduced genera include *Halimus* Wallroth (1822); *Schizotheca* Meyer (ex. Lindley 1846), not *Schizotheca* Ehrenberg (1832); *Phyllotheca* Nuttall (ex. Moquin-Tandon in de Candolle, 1849); *Lophocarya* Nuttall (ex. Moquin-Tandon in de Candolle, 1849); *Pterocarya* Nuttall (ex. Moquin-Tandon in de Candolle, 1849), not *Pterocarya* Kunth (1824); *Phyllocarpa* Nuttall (ex. Moquin-Tandon in de Candolle, 1849), not *Phyllocarpus* Riedel (1842); *Theleophyton* Moquin-Tandon (in de Candolle, 1849); *Armola* Kirschloger (ex. Montandon, 1856); and *Teutliopsis* Celakovsky (1872). Ulbrich (in Engler & Prantl, 1934) has proposed three new generic divisions, all based on members described previously as *Atriplex*. No attempt has been made by the author to evaluate the proposals of Ulbrich,

who proposed *Rumicastrum* based upon *Atriplex chamaecladum* Diels, *Neopreissia* based upon *Atriplex isatidea* Moq. and *Haloxanthium* based upon *Atriplex quadrivalvatus* Diels.

TAXONOMIC CONCLUSIONS

The taxonomy of the shrubby species of *Atriplex* native to the United States is a complex problem due to the limited number of pistillate flower parts and the uniformity of the staminate flowers throughout the group treated. Therefore it is necessary to correlate the morphological characteristics of the branches, twigs and leaves with those of the pistillate flower in order to understand the taxonomy of the group. When, for example, the striately angled twigs of the *A. torreyi* group and the terete twigs of the *A. lentiformis* group are each correlated with their respective leaves and fruits, which are easily confused and attributed to the other group when seen alone, the forms are easily classified and segregated from one another.

McMinn's (1939) treatment of *A. breweri* has been followed in its reduction to varietal rank under *A. lentiformis*. Its apparent geographical segregation from *A. lentiformis* plus the minute differences in the shape and size of its leaves, the difference in the transparency of the mature fruiting bracts, and the amount of monoeciousness present serve to segregate these entities. Otherwise the two are strikingly similar in habit.

In the *torreyi* group, *A. griffithsii* has been reduced to a variety of *A. torreyi* because of the characteristic striately angled twigs. From the literature seen, *A. torreyi* var. *griffithsii* appears to be smaller in stature than *A. torreyi* and so with a more liberal treatment it could be maintained as a distinct species.

A. macropoda was reduced to a subspecies of *A. canescens* by Hall (1923), and judging by the three collections seen, including the type, there are apparently no differences in its morphology, aside from more sponginess in the united body of the fruiting bracts, to merit its status as being a separate subspecies of *A. canescens*. Otherwise, it appears to be *A. canescens* var. *macilenta*. The type of *A. canescens* var. *macilenta* and two isotypes have been examined. *Macilenta* is the earliest legitimate epithet for the *linearis* group but commonly it has been rejected as *nomen dubium* due to the immaturity of the isotypes. The type has numerous nearly mature fruiting bracts, and clearly it represents the common plant well-known var. *linearis*.

Due to its subshrubby nature (the annual stems dying back to a woody base), *A. aptera* (*A. canescens* subsp. *aptera*) has not been included in the *canescens* complex. It is the author's opinion that this entity should be given a thorough taxonomic study along with other members of the North America subshrubby *Atriplex* in order that its correct position in the genus may be ascertained. Hall (1923) may be correct in stating that *A. aptera* may be a hybrid between *A. canescens* and *A. nuttallii*. If this is true, then *A. aptera* should be associated with *A. nuttallii* as a subshrub rather than with *A. canescens* as a shrub.

Fortunately, most of the members of the group treated do not seem to intergrade with one another. The exceptions are the entities in the *canescens* group and probably *A. lentiformis* and its var. *breweri*. One finds variation from one variety of the group to the other extreme in each of these groups.

There has been found however, one case of almost unmistakable hybridization between two apparently incompatible entities, *A. confertifolia* and *A. canescens*. The plant, found growing among typical *canescens* and *confertifolia* plants, was collected by the late H. M. Hall on the buttes west of Winslow, Arizona (*Hall* 11176, GH, UC).

Methods of Study

The principal method of study and basis for revision was a meticulous examination of approximately 3000 specimens, some in the Herbarium of Pomona College and many from various other herbaria in the United States.

This study was fully complemented with field studies during the past two years. The excursions were made principally in Southern California where all but two of the entities (*A. canescens* var. *garrettii* and *A. torreyi* var. *griffithsii*) are found. A total of 182 sheets including all but the two varieties were collected and were deposited in the Herbarium of Pomona College.

Acknowledgments.—The writer wishes to express his appreciation for the advice and guidance by Dr. Lyman Benson, Professor of Botany at Pomona College, who also suggested the study of the group treated. The writer wishes to thank the curators of the following herbaria (abbreviations given are those used in citation of specimens) for the specimen loans of the group treated: Herbarium of the California Academy of Sciences, San Francisco—CAS; Dudley Herbarium, Stanford University—DS; Gray Herbarium, Harvard University—GH; Herbarium of the New York Botanical Garden—NY; Herbarium of Pomona College—POM; Rocky Mountain Herbarium, University of Wyoming—RM; Herbarium of the University of California, Berkeley—UC; United States National Herbarium—US; Vegetation Type Map Herbarium, University of California, Berkeley —VTM.

Atriplex L.

Atriplex L. Sp. Pl. 1052. 1753. *Obione* Gaertn. Fruct. 2:198. 1791. *Pterochiton* Torr. & Frem. in Frem. Rept. Expl. Exped. Rocky Mts. & Ore. Calif. 318. 1845.

Annual or perennial herbs or shrubs; herbage usually more or less furfuraceous; leaves alternate or opposite, sessile or petioled, entire, dentate, or serrate or irregularly lobed or cleft; flowers monoecious or dioecious, solitary or clustered, axillary or in terminal spikes or panicles, the staminate and pistillate flowers mixed in the inflorescence or the staminate axillary glomerules superior to or terminal to the pistillate axillary glomerules; staminate flowers ebracteate but with a 3-5-parted perianth, the segments oblong or obovate, obtuse, the 3-5 stamens inserted on the perianth base, the filaments united at the base or distinct, the anthers 2-celled, the rudimentary ovary conical or wanting; pistillate flowers each subtended by 2 bracts which enclose the fruit, distinct or united, fleshy, spongy or ligneous, the margins entire or variously indented, the backs smooth or variously appendaged, the perianth none or rarely of 1-5 squamellae or a 3-5-lobed membranaceous calyx, the stamens wanting; ovary ovoid or depressed-globose; stigmas 2, subfiliform, but thickened or compressed near the connate bases; the ovule either oblique or erect and with a short funiculus or inverted and suspended from the end of an elongated funiculus; utricle with a membranaceous pericarp, this usually free from the seed; seed erect or inverted, rarely horizontal, the coats membranaceous, coriaceous, or subcrustaceous; embryo annular around the farinaceous endosperm, the radicle inferior, lateral or superior.

Species about 130, common in alkaline habitats, widely scattered over the Earth. Type species, *Atriplex hortensis* L.

Formal Treatment of Some Native Shrubs of the Genus Atriplex

Shrubs; foliage and young stems furfuraceous because of the drying out of the epidermal vesicular hairs; leaves alternate, sessile or petioled, entire, dentate or serrate or irregularly lobed, subtending axillary flower clusters and undeveloped branches; leaves of undeveloped branches reduced; flowers dioecious, rarely monoecious (commonly so in *A. lenti-*

formis var. *breweri*), clustered, axillary or in terminal panicles, the staminate and pistillate flowers of monoecious plants mixed in the inflorescence; staminate flowers with a 4-5-parted perianth, the segments oblong, obtuse, the filaments flattened and scarious margined, more or less united at the base; pistillate flowers without perianth; fruiting bracts united, spongy or ligneous; ovary of the fruit ovoid; ovule inverted and suspended from the end of an elongated funiculus; seed inverted, the coats crustaceous, the radicle superior or rarely lateral.

Species eight; western United States and northern Mexico.

KEY TO SPECIES TREATED

1. Leaves with an irregularly undulate or coarsely, deeply and saliently toothed margins ..... 1. *A. hymenelytra*
1. Leaves entire
2. Fruiting bracts smooth, not winged or tubercled dorsally
3. Branches and twigs not striately angled but terete, becoming spiny
4. Fruiting bracts 5-16 mm long, 3-10 mm wide, with free, divergent, herbaceous tips
5. Fruiting bracts globose and subligneous around the fruit, the free, herbaceous tips obovate, constricted basally ..... 2. *A. spinifera*
5. Fruiting bracts convex and ligneous around the fruit, the free, ovate and herbaceous tips not constricted basally ..... 3. *A. confertifolia*
4. Fruiting bracts 2-3 mm long, 3-5 mm wide, with short, broad and thickened tips ..... 4. *A. parryi*
3. Branches and twigs either striately angled and sometimes becoming spiny or terete and not becoming spiny
4. Branches and twigs striately angled ..... 5. *A. torreyi*
4. Branches and twigs terete ..... 6. *A. lentiformis*
2. Fruiting bracts longitudinally winged or tubercular-crested dorsally, rarely smooth
3. Fruiting bracts 2-3 (rarely 5) mm long, 2-4 (rarely 6) mm wide, each side commonly with two tuberculately appendaged crests or rarely smooth ..... 7. *A. polycarpa*
3. Fruiting bracts 5-15 (occasionally 20) mm long, 4-15 (occasionally 25) mm wide, each side with 2 entire, serrate, laciniate, dentate, or laciniately or fimbriately cleft or divided wings ..... 8. *A. canescens*

1. ATRIPLEX HYMENELYTRA (Torr.) S. Wats.

Obione hymenelytra Torr. Pac. R. R. Rept. 4:129. 1857. *A. hymenelytra* S. Wats. Proc. Amer. Acad. 9:119. 1874.

Shrub, to 1 m tall, compactly branching, rounded; twigs brittle, not becoming spiny; leaves commonly orbicular in outline, the margins irregularly undulate or coarsely, deeply, and saliently toothed, 18-30 mm long, 20-35 (rarely 45) mm wide, with a persistent silvery-white scurf, the petioles 3-10 mm long; fruiting bracts 5-13 mm long, 5-14 mm wide, united below the seed into a spongy, club-shaped stalk, free, round-reniform, and little divergent above, the free margins entire to denticulate, the sides smooth; seed oval, 1-1.8 mm long, 1.6-2 mm wide, the radicle superior or nearly lateral.

Dry alkaline alluvial fans and hills at -270 to 3,900 feet elevation; Owens Valley, California, to southwestern Utah; southward through the Mojave and Colorado deserts in California, southern Nevada, and northwestern Arizona.

Representative specimens.—CALIFORNIA. INYO CO.: West side of Townes Pass, Panamint Mts., *Eastwood & Howell* 7692, CAS. KERN CO.: Iron Canyon, El Paso Mts., *Weston* in 1926, CAS. SAN BERNARDINO CO.: Silver Lake, *Thompson* 50, CAS. RIVERSIDE CO.: Dos Palmas, *Gentry* in 1933, DS. SAN DIEGO CO.: Near Palm Wash, west Colorado Desert, *J. T. Howell* 3517, CAS. IMPERIAL CO.: ¼ mile north of base of Signal Mt., *C. B. Wolf* 2180, DS. NEVADA. CLARK CO.: Gypsum Cave, *Munz* 14913, GH, POM. ARIZONA. YUMA CO.: Hyder, *Peebles* 12028, POM, US. MARICOPA CO.: Agua

Caliente, *Carlson* in 1914, CAS. MEXICO. BAJA CALIFORNIA: Cucopa Mts., *MacDougal* 143, NY.

Type collection.—ARIZONA. "On the Gila," *Fremont* in 1849. Type, NY, photograph, POM. *Fremont* in 1849, NY, is designated as the lectotype.

2. ATRIPLEX SPINIFERA Macbr.

A. spinifera Macbr. Contr. Gray Herb. (53):11. 1918. *Obione spinifera* Ulbrich in Engl. & Prantl Naturl. Pflanzenf. ed. 2, 16C:508. 1934.

Shrub, to 1 m tall, densely and rigidly branched, taller than broad; branches and twigs becoming rigid, divergent spines; leaves ovate or ovately subhastate, 11-35 mm long, 5-16 mm wide, the apex acute, the petioles 1-5 mm long; fruiting bracts obovate in outline, 5-16 mm long, 3-10 mm wide, united, globose and subligneous around the fruit, free, obovate, herbaceous and divergent above, constricted basally, the margins entire or commonly palmately-lobulate, the sides smooth; seeds ovate, 2.1-2.9 mm long, 1.1-1.7 mm wide.

Dry alkaline hills and flats at 100 to 4,100 feet; western San Joaquin Valley and western Mojave Desert, California.

Representative specimens.—CALIFORNIA. MERCED CO.: Volta, *Annard* in 1929, DS, POM. FRESNO CO.: 3 miles south of South Dos Palos, *H. M. Hall* 11021, GH, NY, UC. KINGS CO.: 4 miles west of Lemoore, *Hoover* 3333, UC, US. SAN LUIS OBISPO CO.: Between Simmler and Soda Lake, *Ferris & Rossbach* 9462, DS, GH, UC. KERN CO.: Lost Hills, *Abrams* 13816, DS, UC. LOS ANGELES CO.: Near Lancaster, *M. E. Jones* in 1925, POM. SAN BERNARDINO CO.: Victorville, *Covel* in 1940, CAS.

Type collection.—CALIFORNIA. KERN CO.: "Maricopa hills," *Eastwood* 3269. Type, GH, photographs, NY, POM, US; isotype, US.

3. ATRIPLEX CONFERTIFOLIA (Torr. & Frem.) S. Wats.

Obione confertifolia Torr. & Frem. in Frem. Rept. Ore. & Calif. 318. 1845. *O. rigida* Torr. & Frem. in Frem. Rept. Ore. & Calif. 156. 1845, *nomen nudum*. *O. spinosa* Moq. in DC. Prodr. 13(2):108. 1849. *A. spinosa* Dietr. Syn. Pl. 5:536. 1852. *A. confertifolia* S. Wats. Proc. Amer. Acad. 9:119. 1874. *A. collina* Woot. & Standl. Contr. U. S. Nat. Herb. 16:119. 1913. *A. subconferta* Rydb. Fl. Rocky Mts. 248. 1917.

Shrub, to 1 m tall, rigidly branched, rounded; branches and twigs becoming spiny; leaves ovate, obovate or rarely elliptic, commonly caducous, 12-41 mm long, 8-21 mm wide, entire, the apex obtuse or rounded, the petioles 1-7 mm long, the axillary bud leaves ovate or obovate to elliptic, 1-12 mm long, 1-7 mm wide, persistent; fruiting bracts ovate or elliptic, 5-13 mm long, 5-10 mm wide, convexly united and ligneous around the fruit, free, ovate, herbaceous and divergent above, not constricted basally, the margins entire, rarely undulate, denticulate, or serrulate; seeds oval, 1+-2+ mm long, 1—-2 mm wide.

Widely spread over desert valleys and hills at 1,800 to 6,700 feet elevation; eastern Oregon to western North Dakota; southward to the Mojave Desert, northern Arizona and northwestern New Mexico; Presidio County, western Texas (one specimen).

Representative specimens.—OREGON. GRANT CO.: Humphrey's Ranch, *Henderson* 5022, CAS, GH. LAKE CO.: Near Alkali Lake, *J. W. Thompson* 12171, CAS, DS, POM, US. WHEELER CO.: 3 miles west of Mitchell, *Peck* 18639, NY (2). IDAHO. LEMHI CO.: 15 miles south of Salmon, *Hitchcock, Rethke, & Raadshooven* 3719, CAS. BANNOCK CO.: Pocatello, *Palmer* 444, GH, US, 539, US, 434, US. MONTANA. DAWSON CO.: Colgate, *Sandberg* 8947, UC. NORTH DAKOTA. BILLINGS CO.: Tracy Mountain, *Stevens* 484, UC, US. WYOMING. SHERIDAN CO.: Dayton, *F. F.* 2454, NY. NATRONA CO.: Powder River, *Nelson* 9420, GH, NY. CARBON CO.: Fort Steele, *Nelson* 4824, POM. CALIFORNIA. LASSEN CO.: Wendel, *Hoover* 4663, UC, US. MONO CO.: Paoha Island, *Gifford* 860, UC, VTM. INYO CO.: Above the forks of Silver Canyon, White Mts., *Applegate* 6933, DS; Silver Canyon, White Mts., *Duran* 3156, CAS, DS, GH, NY, POM, UC, US. KERN CO.: ¼ mile south of Rosamond, *C. B. Wolf* 2624,

POM, US. NEVADA. WASHOE CO.: Steamboat Springs, *Rose* 35557, NY, POM, UC, *Heller* 10366, GH. CLARK CO.: 10 miles southeast of Las Vegas, *Maguire* 13579, GH. UTAH. JUAB CO.: Tintic Valley, *Harris* C2595, POM. SAN JUAN CO.: Junction of Nokai Creek and San Juan River, *Cutler* 2275, CAS, GH, US. COLORACO. MOFFAT CO.: Maybell, *Cary* 20, US. ADAMS CO.: Denver, *Tracy & Adams* 853, NY. PUEBLO CO.: Pueblo, *Woodward* in 1883, GH. ARIZONA. GRAHAM CO.: 15 miles east of Safford, *Gould & Haskell* 4011, UC, US. NEW MEXICO. SAN JUAN CO.: Shiprock, *Brass* 14363, GH. MCKINLEY CO.: South of Gallup, *Wooton* 2769, US (2). TEXAS. PRESIDIO CO.: Bluffs near mouth of Capote Creek, *Havard* in 1883, US.

Type collections.—(1) *Obione confertifolia* Torr. & Frem. UTAH. WEBER CO.: "Borlers of the Great Salt Lake" (near the mouth of the Weber River), *Fremont* 761. Type, NY, photograph, POM. (2) *Obione rigida* Torr. & Frem., *nom. nud.* UTAH. WEBER CO.: "On an island in the Great Salt Lake," *Fremont* 767. Type, NY, photograph, POM. (3) *Obione spinosa* Moq., collected by Nuttall in the Columbia River basin; depository of the specimen(s) is probably the British Museum of Natural History in London. (4) *Atriplex collina* Woot. and Standl. ARIZONA. APACHE CO.: "Dry hills, Navajo Indian Reservation, about north end of the Carrizo Mountains," *Standley* 7481. Type, US, photographs, GH, NY, POM, UC. (5) *Atriplex subconferta* Rydb. IDAHO. "Dry bench lands, Twin Falls and Shoshone Fall," *Nelson and MacBride* 1379. Type, NY, photograph, UC; isotypes, GH, POM, RM, UC, US.

4. ATRIPLEX PARRYI S. Wats.

A. parryi S. Wats. Proc. Amer. Acad. 17:378. 1882. *Obione parryi* Ulbrich in Engl. & Prantl, Naturl. Pflanzenf. ed. 2, 16C:508. 1934.

Shrub, 2-5 dm tall, erect, rounded and rigidly branched; twigs becoming spiny; leaves orbicular-cordate, sessile, 7-16 (rarely 22) mm long, 6-11 (rarely 16) mm wide, entire, the apex obtuse, rarely acute; fruiting bracts cuneate, spongy, 2-3 mm long, 3-5 mm wide, united to above the middle, the free terminal tips thickened and short but broad, the margins entire or serrulate, the sides smooth; seeds 1.3-1.9 mm long, 1.1-1.8 mm wide.

Alkaline flats at 200 to 3,800 feet elevation; Owens Valley, California, to northwest Esmeralda County, Nevada; southward to northeastern Los Angeles County, California, and to west central San Bernardino County, California.

Representative specimens.—CALIFORNIA. INYO CO.: Near Lone Pine, *M. E. Jones* in 1926, NY, POM. KERN CO.: Margin of Dry Lake, Rosamond, *Davy* 2946, UC, US. LOS ANGELES CO.: 2 blocks west of center of town of Lancaster, *C. B. Wolf* 4084, UC, US. SAN BERNARDINO CO.: Near Troy, *Munz, Harwood, & Johnson* 4092, POM, UC, US. NEVADA. ESMERALDA CO.: Northeast branch of Fish Lake Valley, near Cap Spring, *Archer* 7244, NY (2). NYE CO.: Beattie, *Heller* 10421, CAS, GH, NY, US.

Type collection.—CALIFORNIA. LOS ANGELES CO.: Lancaster (cf. Parish, Zoe 5:113. 1901.), *Parry* 282. Type, GH, photograph, POM.

5. ATRIPLEX TORREYI S. Wats.

Shrub, 1.3-2 m tall, densely and divaricately branched; twigs slender or stout, striately angled, becoming spiny or not; leaves narrowly-ovate or oblong, elliptic ovate, ovate, triangular-ovate or subhastate, 12-32 mm long, 4-20 mm wide, entire, the apex obtuse, rounded, mucronulate or acute, the base truncate or tapering, the petiole 1-4 (rarely 5 or 6) mm long; fruiting bracts orbicular, subreniform or cordate-reniform, united at the base, 1-4.5 mm long, 2-5 mm wide, subscarious over the seed when mature so darkness of seed usually discernible or not subscarious, the sides smooth, the margins crenulate or occasionally entire, not divergent; seeds 0.9-1.8 mm long, 1-1.9 mm wide, the radicle superior or rarely lateral.

KEY TO THE VARIETIES OF ATRIPLEX TORREYI

1. Twigs stout or slender, often becoming spiny; leaves triangular-ovate or often subhastate with a truncate base, occasionally ovate, rarely narrowly ovate, the petioles 2-4 (rarely

5 or 6) mm long; fruiting bracts orbicular or subreniform, 1-3.8 mm long, 2-4.6 mm wide, subscarious over the seed when mature so darkness of seed usually discernible ..... 5a. var. *torreyi*

1. Twigs slender, not becoming spiny; leaves ovate to narrowly oblong or occasionally elliptic-ovate, the petioles 1 (rarely 2) mm long; fruiting bracts cordate-reniform, 3-4.5 mm long, 3.5-5 mm wide, not subscarious when mature so darkness of seed not discernible ..... 5b. var. *griffithsii*

5a. ATRIPLEX TORREYI S. Wats. var. TORREYI

Obione torreyi S. Wats. in King. Rept. U. S. Geol. Surv. 40th Par. 5:290. 1871. *A. torreyi* S. Wats. Proc. Amer. Acad. 9:119. 1874. *A. lentiformis* S. Wats. subsp. *torreyi* H. M. Hall in Hall & Clements, Carnegie Inst. Wash. Publ. (326):336. 1923. *A. lentiformis* S. Wats. var. *torreyi* McMinn, Ill. Man. Calif. Shrubs 113. 1939.

Shrub, 1-2 m tall, densely and divaricately branched; twigs stout or slender, striately angled, often becoming spiny; leaves triangular-ovate or often subhastate with a truncate base, occasionally ovate, rarely narrowly ovate, 13-32 mm long, 6-20 mm wide, the apex obtuse, rounded, mucronulate or occasionally acute, the petioles 2-4 (rarely 5 or 6) mm long; fruiting bracts orbicular or subreniform, united at base, 1-3.8 mm long, 2-4.6 mm wide, subscarious over the seed when mature so darkness of seed usually discernible, the sides smooth, the margins crenulate or occasionally entire, not divergent; seeds 0.9-1.8 mm long, 1-1.7 mm wide, the radicle superior or rarely lateral.

Alkaline flats and river benches at 1,800 to 5,500 feet elevation; Washoe County, Nevada, and eastward to Lander County, Nevada; southward through the Owens Valley and into the Mojave Desert; eastward from Los Angeles County, California, through Clark County, Nevada, to southwestern Utah.

Representative specimens.—CALIFORNIA. INYO CO.: Silver Canyon, White Mts., *Duran* 3154, CAS, DS, GH, NY, POM, UC, US. LOS ANGELES CO.: Lancaster, *Wells* in 1909, POM. SAN BERNARDINO CO.: Box "S" Ranch, Lucerne, *Munz & Youngberg* 14960, CAS, GH, POM, UC. NEVADA. WASHOE CO.: West side of Lake Winnemucca between Nixon and Gerlach, *Murphy* 56, UC. PERSHING CO.: Lovelock's, *M. E. Jones* in 1901, POM. UTAH. WASHINGTON CO.: Rockville, *M. E. Jones* in 1894, POM. ARIZONA. MOHAVE CO.: 4 miles east of Beaver dam, *M. E. Jones* 5024at, US.

Type collection.—NEVADA. HUMBOLDT CO.: "Sterile saline plains, Humboldt Co., Nevada," *Torrey* 463. Type, GH, photograph, POM; isotypes, NY (2).

5b. Atriplex torreyi S. Wats. var. griffithsii (Standl.) comb. nov.

A. griffithsii Standl. N. Amer. Fl. 21:63. 1916. *A. lentiformis* S. Wats. subsp. *griffithsii* H. M. Hall in Hall & Clements, Carnegie Inst. Wash. Publ. (326):336. 1923. *A. lentiformis* S. Wats. var. *griffithsii* L. Benson, Amer. J. Bot. 30:236. 1943.

Shrub, 0.3-1 m tall, densely and divaricately branched; twigs slender, striately angled, not becoming spiny; leaves narrowly ovate to narrowly oblong or occasionally elliptic-ovate, 12-27 mm long, 4-11 mm wide, the apex obtuse or rounded, mucronulate, the base usually tapering to the petiole, the petioles 1 (rarely 2) mm long; fruiting bracts cordate-reniform, united at base, 3-4.5 mm long, 3.5-5 mm wide, not subscarious when mature so darkness of seed not discernible, the sides smooth, the margins crenulate or occasionally entire, not divergent; seeds 1-1.5 mm long, 1.4-1.9 mm wide, the radicle superior.

Alkali flats at about 4,000 feet elevation; Willcox Playa, Cochise Co., Arizona, and the Gila River Valley (locality not known), Arizona.

Representative specimens.—ARIZONA. COCHISE CO.: Alkali Flats at Willcox (topotype), collector and date unknown, POM, UC; Willcox Flat, *Shreve* 4239, UC; Willcox, *Griffiths* 1895, fragment, UC, *Darrow* in 1937, CAS; 2 miles west of Willcox, *Parker, Phillips, & Kearney* 6563, CAS, GH, UC; (county not known): Valley of the Gila, *Mohr* in 1871, US; Gila Canyon, *Mohr* 119, US.

Type collection.—ARIZONA. COCHISE CO.: "Wilcox," *Griffiths* 1895. Type, NY (not seen), fragment, UC; isotype, US, photograph, POM.

6. ATRIPLEX LENTIFORMIS (Torr.) S. Wats.

Shrub, to 3 m tall, widely spreading, dioecious or monoecious; twigs terete, rarely becoming spiny; leaves ovate, triangular-hastate or nearly deltoid, 15-40 (rarely 50) mm long, 9-25 (rarely 32) mm wide, entire, the apex rounded or truncate, the base truncate or tapering, the petiole 2-7 (rarely 9) mm long; fruiting bracts orbicular, orbicular-ovate, compressed, sessile or pedicellate, 2-4 (rarely 6) mm long, 2-4.5 (rarely 6) mm wide, united to above the base or above the middle, subscarious over the seed when mature so darkness of seed discernible or not subscarious over the seed and spongy, the margins entire, crenulate or subcrenulate, not divergent, the sides smooth; seeds 0.8-1.6 mm long, 0.9-1.7 mm wide, the radicle superior or rarely lateral.

KEY TO THE VARIETIES OF ATRIPLEX LENTIFORMIS

1. Leaves usually triangular-hastate, or nearly deltoid, less commonly ovate, the apex usually truncate or rounded, the base truncate, less commonly tapering to the petiole; fruiting bracts usually subscarious over the seed when mature so darkness of seed discernible, the margins crenulate, rarely entire; rarely monoecious.....6a. var. *lentiformis*
1. Leaves usually ovate or occasionally triangular-hastate, the apex usually rounded, rarely truncate, the base usually tapering to the petiole; fruiting bracts usually not subscarious over the seed when mature but spongy so darkness of seed rarely discernible, the margins usually entire or sometimes subcrenulate; commonly monoecious.....6b. var. *breweri*

6a. ATRIPLEX LENTIFORMIS (Torr.) S. Wats. var. LENTIFORMIS

Obione lentiformis Torr. in Rept. Exped. Zuni & Colo. Rivers 169. 1853. *A. lentiformis* S. Wats. Proc. Amer. Acad. 9:118. 1874.

Shrub, to 3 m tall, widely spreading, rarely monoecious; twigs terete, rarely becoming spiny; leaves usually triangular-hastate or nearly deltoid, less commonly ovate, 15-30 (rarely 40) mm long, 9-23 (rarely 28) mm wide, entire, the apex usually truncate or rounded, the base truncate, less commonly tapering to the petiole, the petioles 2-7 (rarely 9) mm long; fruiting bracts usually orbicular or orbicular-ovate, compressed, sessile, 2-4 mm long, 2 to 4.5 (rarely 5) mm wide, usually united to above the base or above the middle, usually subscarious over the seed when mature so darkness of seed discernible, the margins crenulate, rarely entire, not divergent, the sides smooth; seeds 1.3-1.6 mm long, 1.1-1.5 mm wide.

Desert slopes and stream bottoms, at -240 to 2,700 feet elevation; southeast Inyo County, California, and eastward to Washington County, Utah; southward to northern Baja California, Mexico, and to northern Sonora, Mexico.

Representative specimens.—CALIFORNIA. INYO CO.: Tecopa Hot Springs, *Munz & Campbell* 14363, RM. IMPERIAL CO.: Mountain Spring, *Palmer* in 1875, GH, 328, NY, UC. NEVADA. CLARK CO.: St. Thomas, *Tidestrom* 8633, NY. UTAH. WASHINGTON CO.: 7 miles east of St. George, *Maguire & Richards* 13306, GH. ARIZONA. PINAL CO.: Sacaton, *Peebles* 7392, CAS, US. MEXICO. BAJA CALIFORNIA: West side Laguna Salada about 20 miles south of border, *Harvey* 1005, DS. SONORA: Valley of the Altar River, *Pringle* in 1884, GH, POM, NY.

Type collection.—CALIFORNIA. "Rio Colorado, Calif.," *Woodhouse* on Nov. 6, 1851. Type, GH, photograph, POM, fragment, UC, one piece of the type specimen is pictured in Sitgr. Rept. pl. XIV. 1853; isotype, NY.

6b. ATRIPLEX LENTIFORMIS (Torr.) S. Wats. var. BREWERI (S. Wats.) McMinn

A. breweri S. Wats. Proc. Amer. Acad. 9:119. 1874. *A. orbicularis* S. Wats. Proc. Amer. Acad. 17:377. 1882. *A. lentiformis* S. Wats. subsp. *breweri* H. M. Hall in Hall

& Clements, Carnegie Inst. Wash. Publ. (326):335. 1923. *A. lentiformis* S. Wats. var. *breweri* McMinn, Ill. Man. Calif. Shrubs 113. 1939.

Shrub, to 3 m tall, widely spreading, commonly monoecious; twigs terete, not becoming spiny; leaves usually ovate or occasionally triangular-hastate, 25 (rarely 20)-40 (rarely 50) mm long, 15 (rarely 12)-25 (rarely 32) mm wide, entire, the apex usually rounded, rarely truncate or acute, the base usually tapering to the petiole, the petioles 2-7 mm long; fruiting bracts orbicular-ovate, compressed, sessile or sometimes pedicellate, especially if plant is monoecious, 2.5-4 (rarely 6) mm long 3-4.5 (rarely 6) mm wide, united to above the base, rarely to the middle or above, usually not subscarious over the seed when mature but spongy so darkness of seed rarely discernible, the margins usually entire or sometimes subcrenulate, rarely crenulate, not divergent, the sides smooth; seeds 0.8-1.3 mm long, 0.9-1.7 mm wide.

Coastal benches, bluffs and valleys and the San Joaquin Valley at 10 to 2,200 feet elevation; southward from the Solano County, California, marshes along the Pacific Coast to Orange County; eastward into the San Benito, Salinas, Santa Maria-Cuyama, Santa Clara, Santa Ana-Cajalco and the Tia Juana Rivers and into the San Joaquin Valley; Santa Cruz, Santa Catalina and San Clemente Islands.

Representative specimens.—CALIFORNIA. SOLANO CO.: Suisun Marshes, *Dudley* in 1905, DS. FRESNO CO.: Firebaugh, *H. M. Hall* 11760, GH, NY, UC. KERN CO.: Near Bakersfield, *Wiggins* 4201, DS, POM, UC. ORANGE CO.: Just north of San Clemente, *C. B. Wolf* 666, DS, US. MEXICO. BAJA CALIFORNIA: Tia Juana, *Diehl* in 1902, POM.

Type collections.—(1) *Atriplex breweri* S. Wats., CALIFORNIA. LOS ANGELES CO.: "Sea Shore-Sta. Monica," *Brewer* 75. Type, GH, photograph, POM, fragment, US; isotypes, UC, US. (2) *Atriplex orbicularis* S. Wats. CALIFORNIA. LOS ANGELES CO.: "Santa Monica," *S. & W. Parish* 1126. Type, GH, photograph, POM; isotypes, DS, US.

7. ATRIPLEX POLYCARPA (Torr.) S. Wats.

Obione polycarpa Torr. Pac. R. R. Rept. 4:130. 1857. *A. polycarpa* S. Wats. Proc. Amer. Acad. 9:117. 1874. *A. curvidens* T. S. Brandg. Proc. Calif. Acad. II. 2:201. 1889.

Shrub, to 1.5 m tall, intricately branched, rounded; twigs delicate, approaching spininess; leaves commonly caducous, obovate or linear ovate, tapering to the base, sessile or subsessile, 6-24 mm long, 2-5 mm wide, entire, the apex obtuse or acute; leaves of the undeveloped branches usually much reduced; fruiting bracts sessile, moderately compressed around the fruit, cuneate-orbicular, usually united to below the middle, 2-3 (rarely 5) mm long, 2-4 (rarely 6) mm wide, the upper margins serrate to deeply toothed, rarely smooth, each dorsal side commonly with two tuberculately appendaged and longitudinal crests or rarely smooth; seeds 1-1.3 mm long, 0.8-1.3 mm wide.

Desert flats and hills at -200 to 4,800 feet elevation; San Joaquin Valley, south of San Benito County, California; eastward to Owens Valley, California, southern Nevada and northwestern Arizona; southward through the Mojave and Sonoran Deserts.

Representative specimens.—CALIFORNIA. SAN BENITO CO.: Tres Pinos Creek near Emmett's Station, *Ferris* 6891, DS. FRESNO CO.: Between Mendota and Coalinga, *H. M. Hall* 11763, GH, UC. SAN DIEGO CO.: San Felipe Canyon, *Buttle* in 1915, CAS, *Palmer* 333, GH, NY. ARIZONA. PINAL CO.: Sacaton, *Peebles* 10599, POM, *M. E. Jones* 24812, CAS, GH, POM, *Kearney* 4, US. PIMA CO.: Quitovaquito, *Mearns* 251, US, 195, US. MEXICO. BAJA CALIFORNIA: 29 miles north of Mesquital, *Hammerly* 76, CAS, DS; San Bartolome Bay, *T. S. Brandegee* in 1897, UC.

Type collections.—(1) *Obione polycarpa* Torr., ARIZONA. GRAHAM CO.: "Valley of Gila" (Emory was near the base of Mt. Graham on the date collected; this mountain is about 13 miles southwest of Safford, Graham Co.), *Emory* on Oct. 28, 1846. Type, NY, photograph, POM. (2) *Atriplex curvidens* Brandg., MEXICO. BAJA CALIFORNIA: "Comondu," *Brandegee* in 1889. Type, UC, photograph, POM, fragment, US.

8. ATRIPLEX CANESCENS (Pursh) Nutt.

Shrub, 0.2-2 m tall; herbage furfuraceous or densely so, whitish or grayish, not spiny; leaves sessile or petioled, linear, linear-lanceolate, linear-oblanceolate, lancolate, oblanceolate, ovate, obovate or narrowly so, tapering to the petiole or to the base when sessile, 12-40 (occasionally 55) mm long, 1-20 mm wide, the apex acute, obtuse or rounded, mucronulate or not, the petiole 1-5 mm long when present; fruiting bracts sessile or pedicellate, 5-15 (occasionally 20) mm long, 4-15 (occasionally 25) mm wide, each dorsal side with two longitudinal, entire, serrate, laciniate, dentate or laciniately or fimbriately cleft or divided wings, 1-8 (occasionally 12) mm broad (or rarely none), the pedicel 1-9 mm long or none; seeds ovate, 1.5-3 mm long, 1-2 mm wide, the radicle superior.

KEY TO THE VARIETIES OF ATRIPLEX CANESCENS

1. Leaves sessile, linear, linear-lanceolate, linear oblanceolate, lanceolate, oblanceolate or narrowly ovate
   2. Wings of the fruiting bracts usually more than 3 mm broad; free terminal tips of the fruiting bracts rarely exceeding the wings
      3. Leaves 15-40 (occasionally 55) mm long; wings usually entire or dentate, serrate or laciniate ..... 8a. var. *canescens*
      3. Leaves 12-25 (rarely 30) mm long; wings laciniately or fimbriately cleft or divided ..... 8b. var. *laciniata*
   2. Wings of the fruiting bracts usually 3 mm or less broad; free terminal tips of the fruiting bracts usually exceeding the wings ..... 8c. var. *macilenta*
1. Leaves petioled, ovate or obovate ..... 8d. var. *garrettii*

8a. ATRIPLEX CANESCENS (Pursh) Nutt. var. CANESCENS

Calligonum canescens Pursh, Fl. Amer. Sept. 370. 1814. *A. canescens* Nutt. Gen. 1:197. 1818. *A. ? berlandieri* Moq. Chenop. Enum. 65. 1840. *Obione canescens* Moq. Chenop. Enum. 74. 1840. *O. tetraptera* Benth. Bot. Voy. Sulph. 48. 1844. *Pterochiton occidentale* Torr. & Frem. in Frem. Rept. Ore. Calif. 318. 1845. *P. canescens* Nutt. J. Acad. Phila. II. 1:184. 1847. *O. occidentalis* Moq. in DC. Prodr. 13(2):112. 1839. *O. berlandieri* Moq. in DC. Prodr. 13 (2):114. 1849. *A. occidentalis* Dietr. Syn. Pl. 5:537. 1852. *O. occidentalis* var. *angustifolia* Torr. Bot. Mex. Bound. 184. 1859. *A. canescens* var. *angustifolia* S. Wats. Proc. Amer. Acad. 9:121. 1874. *A. angustior* Cockerell, Proc. Davenp. Acad. 9:7. 1902. *A. tetraptera* Rydb. Bull. Torr. Club. 39:311. 1912.

Shrub, 0.5-2 m tall, rigid; herbage furfuraceous, grayish, not spiny; leaves plane or revolute, narrowly obovate or lanceolate, commonly linear-lanceolate, tapering to a subsessile or sessile base, 15-40 (occasionally 55) mm long, 2-6 (occasionally 11) mm wide, entire, the apex rounded, obtuse, or commonly acute; fruiting bracts 5-15 (occasionally 20) mm long, 5-15 (occasionally 25) mm wide, the ligneous ovoid body united over the seed, the free terminal tips none or sometimes exceeding the wings which are usually well developed, entire, serrate, laciniate, or dentate, 3-8 (occasionally 12) mm broad, the pedicel 1-9 mm long or none.

Desert slopes and valleys at sea level to 7,500 feet elevation; eastern Oregon to Wyoming and western South Dakota; southward into Baja California, Sonora and San Luis Potosi, Mexico.

Representative specimens.—WASHINGTON. SPOKANE CO.: Near Spokane, *Turesson* 41, RM. SOUTH DAKOTA. SHANNON CO.: Sheep Mt. and sandhills south, *Visher* 2349, NY 2389, NY. MONTANA. CLARK CO.: Helena, *Kelsey* in 1889, DS, POM. NEBRASKA. SCOTTS BLUFF CO.: Canyon east of Scotts Bluff, *Rydberg* 326, NY (2), US. CALIFORNIA. LASSEN CO.: Wendel, Hoover 4668, UC, US. SAN DIEGO CO.: Coronado, *Rose* 35322, CAS, NY, POM, UC 35323, CAS, NY, POM, UC, *Spencer* 1896, GH, 1662, GH, POM. KANSAS. GOVE CO.: Canons, *Hitchcock* 440, GH, NY, RM, US. MORTON CO.: Richfield, *Thompson* 166, CAS, GH, NY, UC, US. OKLAHOMA. COTTON CO.: Red River, southwest of Randlett, *Boke* in 1946, RM. TEXAS. ZAPATA CO.: North of

Zapata, *Clover* 1581, NY. MEXICO. SONORA: Near Colonia Oaxaca, *White* 782, GH. SAN LUIS POTOSI: 15 miles northwest of Cedral, *I. M. Johnston* 7612, GH.

Type collections.—(1) *Calligonum canescens* Pursh, SOUTH DAKOTA. LYMAN CO.: "Big bend of the Missouri." This bend is today part of the northeast boundary of Lyman Co. *Lewis* on Sept. 21, 1804. Type, Academy of Natural Sciences, Philadelphia (not seen), photograph, POM. Lewis on Sept. 21, 1804, Academy of Natural Sciences, Philadelphia, is designated as the lectotype. (2) *Atriplex ? berlandieri* Moq. Type collected in Mexico. Not known by whom collected or where deposited. (3) *Obione tetraptera* Benth., "From the coast of California, probably San Diego." Type probably in the Herbarium of the Royal Botanic Gardens, Kew. (4) *Pterochiton occidentale* Torr. & Frem., "... probably from the borders of the Great Salt Lake." UTAH. Fremont in 1843. Type, NY, photograph, POM. *Fremont* in 1843, NY is designated as the lectotype. (5) *Obione occidentalis* var. *angustifolia* Torr., TEXAS. "394, *Obione*, sandy ridges on Rio Grande, 3-5 ft. tall, much branching, June 17, 1852," *Wright* 1742 in 1852. Type, NY, photograph, POM; isotypes, GH, US. *Wright* 1742, NY, is designated as the lectotype. (6) *Atriplex angustior* Cockerell, NEW MEXICO. DONA ANA CO.: "Sand hills, Mesilla Park," *Cockerell* in 1900. Type, US, photograph, POM.

8b. ATRIPLEX CANESCENS (Pursh) Nutt. var. LACINIATA Parish

A. canescens Nutt. var. *laciniata* Parish in Jepson, Fl. Calif. 1:442. 1914.

Shrub, 1-2 m tall; herbage moderately furfuraceous, grayish, not spiny; leaves oblanceolate or linear-oblanceolate, 12-25 (rarely 30) mm long, 2-3 (occasionally 5) mm wide, plane or revolute, sessile or nearly so, entire, the apex acute or commonly rounded; fruiting bracts 6-9 (rarely 15) mm long, 8-11 (rarely 15) mm wide, the ligneous ovoid body united over the seed, the wings fimbriately or laciniately cleft or divided, 4-7 mm broad, exceeding the narrowly oblong or commonly narrowly triangular terminal tips, the pedicel 0-2 mm long.

Alkaline flats and slopes at -200 to 2,700 feet elevation; northeastern Los Angeles County, California, and eastward to Nye County, Nevada; southward to northern Baja California and northwestern Sonora, Mexico.

Representative specimens.—CALIFORNIA. INYO CO.: Near Furnace Creek Ranch, *Gilman* 2129, US. SAN BERNARDINO CO.: Old Woman Springs, *Munz & Johnston* 11205, GH, POM. RIVERSIDE CO.: Caleb, *Parish* 8255, DS, GH, *Ingram* 9, CAS, POM. IMPERIAL CO.: 8 miles west of Plaster City, *G. D. Brown* 499, POM, NEVADA. NYE CO.: Sarcobatus Flat, *Monnet* in 1913, CAS. MEXICO. BAJA CALIFORNIA: Rio Santo Domingo, *Wiggins & Demaree* 4783, CAS. SONORA: 21 miles south of San Luis, *Wiggins* 8591, DS.

Type collection.—CALIFORNIA. RIVERSIDE CO.: "Caleb," *Parish* 8256. Type probably in the Jepson Herbarium, University of California; isotype, GH, fragment, UC, photograph, POM.

8c. ATRIPLEX CANESCENS (Pursh) Nutt. var. MACILENTA Jepson

A. linearis S. Wats. Proc. Amer. Acad. 24:72. 1889. *A. canescens* Nutt. var. *macilenta* Jeps. Fl. Calif. 442. 1914. *A. macropoda* Rose & Standl. N. Amer. Fl. 21:72. 1916. *A. canescens* Nutt. subsp. *linearis* H. M. Hall in Hall & Clements. Carnegie Inst. Wash. Publ. (326):344. 1923. *A. canescens* (Pursh) Nutt. subsp. *macropoda* (Rose & Standl.) H. M. Hall in Hall & Clements, Carnegie Inst. Wash. Publ. (326):344. 1923. *A. canescens* (Pursh) Nutt. var. *linearis* Munz, Man. So. Calif. Bot. 141, 598. 1935.

Shrub, 0.3-1 (rarely 2) m tall; foliage and young stems usually densely furfuraceous, whitish, not spiny; leaves linear, linear-oblanceolate or oblanceolate, 14-30 (rarely 50) mm long, 1-3 (rarely 5) mm wide, plane or commonly revolute, sessile or nearly so, entire, the apex acute to rounded or commonly obtuse; fruiting bracts variable, 5-10 mm long, 4-8 mm wide, the ligneous or spongy ovoid body united over the seed, the wings usually dentate or laciniate or rarely none, 1-3 mm broad, the free terminal tips exceeding the wings, commonly broadly oblong to nearly linear, often 3-dentately lobed, 1-3 (rarely 5) mm long, 0.5-3 mm wide, the pedicel 0-4 (rarely 7) mm long.

Coastal (Baja California and Sonora) and desert alkaline flats and allu-

vial fans at -200 to 2,300 feet elevation; Mojave Desert; eastward to Tucson, Arizona; southward through Baja California and Sonora, Mexico.

Representative specimens.—CALIFORNIA. INYO CO.: 2½ miles southeast of Stovepipe Wells, *G. D. Brown* 466, POM. LOS ANGELES CO.: Lancaster, *Parry* 281½, GH. IMPERIAL CO.: Wister, *C. B. Wolf* 4330, GH. ARIZONA. PINAL CO.: Sacaton, *Kearney* 5, US. MEXICO. BAJA CALIFORNIA: San Bartolome Bay, *J. T. Howell* 10668, CAS, DS. SONORA: Subuoral, *Wiggins & Rollins* 252, DS, RM, UC.

Type collections.—(1) *Atriplex linearis* S. Wats., "In alkaline soil about Guaymas. (120, 121, 235)." MEXICO. SONORA: "Plains in alkaline soil," Guaymas, *Palmer* 235. Type, GH, photograph, POM. *Palmer* 235, GH, is designated as the lectotype. "Garden fences in alkaline soil," Guaymas, *Palmer* 120, paratypes, GH, US, photograph of US specimen, GH, 121, GH. (2) *Atriplex canescens* var. *macilenta* Jeps., CALIFORNIA. IMPERIAL CO.: "Bluffs of the Alamo, Calexico," *Parish* 8258. Type in the Jepson Herbarium, University of California, UC; isotypes DS, photograph, POM, GH. (3) *Atriplex macropoda* Rose and Standl., MEXICO. BAJA CALIFORNIA: "Pichilinque Island," *Rose* 16578. Type, US, photographs, GH, POM.

8d. ATRIPLEX CANESCENS (Pursh) Nutt. var. GARRETTII (Rydb.) L. Benson

A. garrettii Rydb. Bull. Torrey Club 39:312. 1912. *A. canescens* Nutt. subsp. *garrettii* H. M. Hall in Hall & Clements, Carnegie Inst. Wash. Publ. (326):344. 1923. *A. canescens* Nutt. var. *garrettii* L. Benson, Amer. J. Bot. 30:326. 1943.

Shrub, 0.2-0.8 m tall; herbage densely furfuraceous, grayish, not spiny; leaves petioled, ovate to obovate, 20-30 mm long, 10-20 mm wide, narrowed and acute to the petiole, the apex obtuse or rounded, often mucronulate, the petiole 1-5 mm long; fruiting bracts sessile or pedicellate, 6-9 mm long, 6-8 mm wide, the ligneous ovoid body united over the seed, the wings dentate, entire or rarely laciniate, 2-5 mm broad, exceeding the free terminal mucronulate tips, the pedicel 1-2 mm long or none.

Desert flats and river benches at 3,000 to 4,800 feet elevation; southeastern Utah; southwestern Colorado; northeastern Arizona; and northwestern New Mexico.

Representative specimens.—UTAH. SAN JUAN CO.: Junction of Nokai Creek and San Juan River, *Cutler* 2281, CAS, GH, US; Moab, *M. E. Jones* in 1913, POM; Colorado River, north of Moab, *Holmgren & Hansen* 3494, GH, NY, US. COLORADO. MESA CO.: Palisade, *Crandall* 112, GH. MONTEZUMA CO.: Mancos, *Baker, Earle & Tracy* 420, US. ARIZONA. COCONINO CO.: Navajo Bridge, *Eastwood & Howell* 6488, CAS, *Barkeley & Reed* 4367, GH, NY, *L. Benson* 13518, POM; Lees Ferry, *M. E. Jones* in 1890, POM, *Jaeger* in 1927, POM. NEW MEXICO. (County not known): Tiznitzin, *Wooton* 2775, US.

Type collection.—UTAH. SAN JUAN CO.: "Moab and vicinity," *Rydberg & Garrett* 8465. Type, NY (not seen); isotype, US, photograph, POM.

A Revision of the Rosa Californica Complex

Donald Cole

Pomona College, Claremont, California

The Genus *Rosa* was described by Linnaeus in his *Species Plantarum* in 1753. *R. centifolia* has been designated as the standard or type species (Briquet, 1935). The Genus, native to the Northern Hemisphere, is common in both the Old and New Worlds, probably including from 100 to 200 species. Several workers since the time of Linnaeus have contributed their efforts toward establishing a system of classification for the species falling within this genus. Numerous difficulties have been encountered, however, leading to great differences of opinion as to the number of species. These difficulties are due to the fact that there is a great deal of variation within the major populations and also some intergradation occurring where these populations meet. These factors have led some authors to consider minor variants as well as some of the intergrades as separate taxa.

One of the earliest works on the genus was that of Lindley (1820). In his monograph he recognized 78 species, 14 of which he considered American. Only *R. woodsii*, named and described by him, is related closely to a segment of the group presented in this study. Crepin studied the entire genus. His treatment of American species was based almost entirely upon herbarium specimens, although he did receive from Sereno Watson some information concerning habitat and growing conditions.

Watson (1885) was among the first to treat the North American group of species as a whole. His work included a history and revision of the North American members of the genus. One of the most thorough studies on the genus in North America was undertaken by Rydberg (1918). He recognized 129 species including many new entities which he named and described. A great deal of his work was based upon herbarium studies and correspondence with other workers in the field. One of the greatest contributions to this subject was made by Erlanson (1929, 1934, 1938), who carried on experimental work in the field. Her studies revealed the close relationship of many of the entities and showed how some which had been previously segregated were only phases of larger populations. Her work also established the fact that intergradation does occur when certain entities are brought together. Studies were made on the genus in the Pacific Northwest by Jones (1935) and St. John (1937).

In taking up a group of Western American species centering around *R. californica*, the writer has attempted to present a system which is practical and usable.

Methods of Study

This work included the study of approximately 4,000 herbarium specimens borrowed from the herbaria which are listed below. The writer wishes to thank the curators of these herbaria for the use of their material.

CAS—Herbarium of the California Academy of Sciences, Golden Gate Park, San Francisco; Cl-UC—Clokey Herbarium deposited at the Herbarium of the University of California, Berkeley; DS—Dudley Herbarium, Stanford University, California; GH—Gray Herbarium, Harvard University, Cambridge, Massachusetts; NY—Herbarium of the New York Botanical Garden, Bronx Park, New York City; POM—Herbarium of Pomona College, Claremont, California; OSC—Herbarium of Oregon State College, Corvallis; UC—Herbarium of the University of California, Berkeley; UO—Herbarium of the University of Oregon, Eugene; US—United States National Herbarium, United States Museum, Smithsonian Institution, Washington, D. C.; UTC—Herbarium of the Utah State Agricultural College, Logan; VTM—Vegetation Type Map Herbarium, University of California, Berkeley; WASH—Herbarium of the University of Washington, Seattle; WILLU—Herbarium of Willamette University, Salem, Oregon; WSC—Herbarium of Washington State College, Pullman.

Original publications, as well as other reference material on the subject, were studied at the Pomona College Botany Library. In addition further bibliographic studies were made at the University of California at Los Angeles, the Rancho Santa Ana Botanic Garden, and the Allan Hancock Foundation of the University of Southern California.

Studies of the plants in the field were made in the hills around Lake Henshaw, San Diego County; in the San Gabriel Mountains at Jackson Lake; in the San Bernardino Mountains near Big Bear Lake; and on the Mojave Desert at Box "S" Springs.

Acknowledgments.—The writer wishes to express his appreciation and gratitude to Dr. Lyman Benson to whom he is indebted for guidance and inspiration and for his aid in obtaining materials for study from other institutions.

The writer wishes to express his appreciation to Dr. Philip A. Munz for advice as well as for use of the library and herbarium of the Rancho Santa Ana Botanic Garden.

INTERGRADATION

One of the problems encountered in the study of this group was that of intermediate forms between species. In various regions, where physical barriers break down, large populations come in contact with one another. If the environmental conditions are right, plants from these populations may produce intermediate forms which grow between the populations and on the peripheries of the species areas. One of the largest and most complex areas of intergradation for this group is the Pit River Region of northern California and in adjacent southern Oregon. Here the vegetation of the Sagebrush Desert of the Great Basin comes in contact with the vegetation of woodlands and forests of the Pacific Slope. Three species of the genus *Rosa* intergrade with one another in this region: *R. californica* from the south, *R. pisocarpa* from the northwest, and *R. woodsii* var. *ultramontana* from the Sagebrush Desert to the southeast. Specimens showing morphological characters of all three taxa were not observed definitely in herbarium studies. However, it is possible that some plants growing in this region do exhibit characters of all three. A species named and described by Greene (1912) as *R. copelandii* appears to be an intermediate between *R. californica* and *R. pisocarpa*, and others combine the distinctive characters of *R. californica* and *R. woodsii* var. *ultramontana*. The following specimens are cited as examples of intergrades occurring in this region:

R. californica X *R. pisocarpa*.—OREGON. JOSEPHINE CO.: Waldo, *D. Kildale* 7928 (DS), *A. Eastwood* 2104 (US); Grants Pass, *M. E. Peck* 2151 (WILLU). JACKSON

CO.: Pinehurst, *E. I. Applegate* 4377 (DS); Elk Creek, few miles from Rogue River, *L. F. Henderson* 13241 (UO); Antelope Creek, *E. I. Applegate* 2379 (US). CALIFORNIA. SISKIYOU CO.: Mt. Eddy, *A. Eastwood* 1969 (US); northeast base Mt. Eddy, Metcalf's Ranch, *A. A. Heller* 13589 (WASH); Sisson, *W. W. Eggleston* 11701 (US); Klamath River, 6 miles north of Hornbrook, *D. K. Kildale* 8371 (DS). HUMBOLDT CO.: along streamlet, Horse Mt., *J. P. Tracy* 9138 (UC).

R. californica X *R. woodsii* var. *ultramontana*.—OREGON. KLAMATH CO.: Lost River, base of Sterkel Mt., *E. I. Applegate* 5155, (DS). HARNEY CO.: Catlow Valley, *R. Drews* in 1937 (UO); 2 miles north of Denio, *M. E. Peck* 25579 (WILLU); Alvord Ranch, *M. E. Jones* 25390, (CAS, DS, POM); CALIFORNIA. SISKIYOU CO.: 6 miles northwest of Callahan, *A. M. Alexander & L. Kellogg* 128, (UC). MODOC CO.: east slope of Warner Mts., Cedar Pass Road, *E. D. Cantelow* 4322 (CAS). SHASTA CO.: Weaverville, *P. L. Johnson* 179 (VTM). LASSEN CO.: 3½ miles southwest of Harvey Mt. Lookout, *A. Simontacchi* 920 (VTM). BUTTE CO.: Snag Lake 7 miles east of Chaparral, *A. A. Heller* 15283 (CAS, CI-UC, DS, WSC). SIERRA CO.: Loyalton, *A. Eastwood* 7898 (CAS). EL DORADO CO.: Glen Alpine Springs Hotel, *W. R. Dudley* in 1900 (DS). MARIPOSA CO.: Stoneman Bridge, Yosemite Natl. Park, *H. M. Hall* 9085 (UC).

R. pisocarpa X *R. woodsii* var. *ultramontana*.—OREGON. KLAMATH CO.: south bank Klamath River, *J. B. Leiberg* 4316 (US); Lake of the Woods, *M. E. Peck* 16503 (WILLU). LAKE CO.: *Lakeview, M. E. Peck* 15260 (WILLU); Poison Creek, Lake Albert, *W. W. Eggleston* 7129 (US). CALIFORNIA. SISKIYOU CO.: Willow Creek, south of Lower Klamath Marsh, *E. I. Applegate* 3919 (DS); Sisson, *L. E. Smith* in 1915 (CAS); Yreka Creek, *G. D. Butler* 1804 (DS, US). SHASTA CO.: Goose Valley, *A. Eastwood* 992 (US).

Along the Columbia Gorge in Western Klickitat County, southern Washington and the Hood River Region of northern Oregon, where the Columbia River passes through the Cascade Mountains, intergrades between *R. pisocarpa* and *R. woodsii* var. *ultramontana* are found. The following specimens are examples:

WASHINGTON. KLICKITAT CO.: Falcon Valley, *W. N. Suksdorf* 7289 (WSC), 7291 (WSC), in 1918 (WSC); Bingen, *W. N. Suksdorf* 10935 (WSC), in 1898 (WSC); Major Creek, *W. N. Suksdorf* in 1886 (GH). OREGON. HOOD RIVER CO.: open woods, Hood River, *M. E. Peck* 2134 (WILLU). WASCO CO.: Eight Mile Creek, *M. W. Gorman* in 1925 (UC); along Ramsey Creek near Dufur, *G. N. Jones* 4194 (WASH).

Specimens which appear to be intergrades between these two entities are also found in various regions east of the Cascade Mountains. The following specimens are examples:

WASHINGTON. CHELAN CO.: Entiat, *G. N. Jones* 1401 (WASH). KITTITAS CO.: Cle Elum, *E. J. Palmer* 37859 (US). OREGON. UMATILLA CO.: Pendleton, *A. A. Heller* 10170 (DS, GH, US); Meacham, *M. E. Peck* 6388 (WILLU), 6590 (WILLU). UNION CO.: La Grande, *M. E. Peck* 2162 (WILLU); Telocast, *M. E. Peck* 6190 (WILLU). CROOK CO.: Prineville, *F. V. Coville & E. I. Applegate* 673 (US).

KEY TO THE SPECIES

A. Hypanthium covered with gland-tipped hairs; plants very small, 2 dm high or less ..... 1. *R. spithamea*

A. Hypanthium not covered with gland-tipped hairs; plants usually large and shrubby, usually 1 m or more in height ..... B

B. Stems usually armed with stout, flattened, recurved prickles; pedicels villous; hypanthium often pilose when young; sepals sometimes pubescent on the backs ..... 2. *R. californica*

B. Stems armed with straight or ascending, weak, narrow prickles; infrastipular prickles rarely stout; pedicels sometimes glandular-hispid, but never villous;

hypanthium glabrous; sepals sometimes glandular-hispid on the backs, not pubescent. C

c. Shrub 5 to 10 dm high; infrastipular prickles stout and long; margins of the leaflets doubly serrate, with gland-tipped teeth; pedicels glandular-hispid. ..... 3. *R. pinetorum*

c. Shrub 1 to 3 m high; infrastipular prickles straight, slender, sometimes ascending; margins of leaflets simply serrate, without gland-tipped teeth; pedicels glabrous. ..... D

d. Stem slender, 1 to 2 m high; armed with few straight often ascending infrastipular prickles; leaflets finely serrate, veins standing out on lower surfaces; sepals glandular-hispid on the backs (West of Cascades and Coast Ranges) ..... 4. *R. pisocarpa*

d. Stem stout, 1 to 3 m high; stem armed with straight, slender, stramineous prickles, sometimes densely so; floral branches often unarmed; leaflets sharply and coarsely serrate, veins usually not standing out on the lower surfaces; sepals rarely glandular-hispid on the backs (East of the Cascade Mountains and the Sierra Nevada) ..... 5. *R. woodsii*

1. ROSA SPITHAMEA S. Wats.

R. spithamea S. Wats. Bot. Calif. 2:444. 1880. *R. sonomensis* Greene, Fl. Fran. 72. 1891. *R. spithamea* S. Wats. var. *sonomensis* (Greene) Jeps. Fl. W. Middle Calif. 279. 1901. *R. adenocarpa* Greene, Leaflets Bot. Obs. & Crit. 2:261. 1912. *R. granulata* Greene, loc. cit. 262. *R. lesterae* Eastw. Leaflets of Western Botany 3:262. 1943.

Low, slender, sparingly branched plant, 1 to 3 dm high; stem densely or sparsely armed, with the longer and stouter prickles infrastipular; floral branches usually armed, with stout, straight infrastipular prickles; stipules short, narrow, glandular-ciliate, sometimes glandular-pruinose on lower surfaces; petiole and rachis sparsely prickly or not prickly, glabrous or puberulent, with stalked glands; leaflets 3 to 7, broadly oval to roundish, rounded at the bases and apices, 0.5 to 2.5 cm long, the margins doubly serrate with gland-tipped teeth, glabrous on both surfaces, sometimes puberulent below, often somewhat glaucous below; flowers in corymbs or solitary; pedicels glandular-hispid; hypanthium densely bristly, 7 to 8 mm thick, 6 to 8 mm long in fruit, globose; sepals glandular-hispid on backs, acuminate, sometimes caudate-attenuate.

In open or shaded woods and forests, Upper Sonoran and Transition zones. Oregon in the Cascade Mountains of Douglas, Josephine, and Jackson counties; California in the Coast Ranges of Humboldt, Trinity, Mendocino, Lake, Marin, and Sonoma counties; Mt. Diablo Range; Santa Cruz Mountains; central Sierra Nevada.

SIGNIFICANT AND REPRESENTATIVE SPECIMENS

Number of specimens examined: 125.

OREGON. DOUGLAS CO.: dry hillside, Oakland, *M. E. Peck* 6595 (WILLU). JOSEPHINE CO.: north slope of Sexton Mt., *M. E. Peck* 19346 (WILLU); Grants Pass, *M. E. Peck* 2158 (WILLU). JACKSON CO.: near Weimer, *E. W. Hammond* 120 (US).

CALIFORNIA. HUMBOLDT CO.: Brannan Mt. near Willow Creek, *L. R. Abrams* 7102 (DS); Trinity River at Hoopa, *D. Kildale* 9549 (DS); Bridgeville, *A. Eastwood* & *J. T. Howell* 4754 (CAS). TRINITY CO.: Trinity River Hyampum to Hoopa, *V. Rattan* in 1883, (DS, GH, US). MENDOCINO CO.: Ukiah, *A. Eastwood* 3376 (CAS); Wolf Creek, *L. R. Abrams* 5902 (DS, WILLU); 6 miles west of Ukiah, *L. R. Abrams* 8147 (DS, POM); Comptche, *H. A. Walker* 309 (UC). LAKE CO.: Elk Mt., *J. P. Tracy* 2343 (UC, US); Whispering Pines Resort, *M. S. Baker* 9711 (CI-UC); northwest of Middletown, *R. F. Hoover* 5329 (UC). SONOMA CO.: Summit of Rose Butte, *M. S. Baker* 11755 (CAS); Petrified Forest, *E. L. Greene* in 1888 (US). NAPA CO.: north side of Mt. St. Helena, *L. Benson* 1931 (POM). MARIN CO.: Mt. Tamalpais, *V. Bailey* 531 (US), *A. Eastwood* 1510, (CAS, GH, US); Lake Lagunitas, *J. T. Howell* 23001

(CAS). CONTRA COSTA CO.: Mt. Diablo, *A. Eastwood* 11705 (CAS). SANTA CLARA CO.: Saratoga, *J. B. Davy* 316 (UC), *L. R. Abrams* 5280 (DS). MONTEREY CO.: Pajaro Hills, *H. P. Chandler* 438 (UC). MERCED CO.: Merced Canyon, *E. D. Cantelow* 4324 (CAS). MARIPOSA CO.: Mariposa Grove, *H. M. Hall* 9672 (UC).

Type Collections: (1) *R. spithamea,* "On Trinity River, very abundant in open woods, 'never more than a foot high,' V. Rattan, July, 1878." Isotype (DS) 49526, photograph (POM). (2) *R. sonomensis,* "Rare montane species, on high dry slopes: Sonoma Co., *Greene;* Mt. Tamalpais, *Jepson;* Saratoga, Santa Clara Co., *Davy.*" (3) *R. adenocarpa,* "known only as collected on Mount Grayback in southwestern Oregon, June 15, by C. V. Piper." Type (US) 527765, photograph (POM). (4) *R. granulata,* "collected on the Calif. Geol. Survey, by Brewer, somewhere near San Luis Obispo, Calif., in April, 1861." Type (US) 320920, photograph (POM). (5) *R. lesterae,* CALIFORNIA. YUBA CO.: on road between Dobbin & Camptonville, *L. Rowntree* in 1941. Type (CAS) 290633, photograph (POM).

2. ROSA CALIFORNICA C. & S.

C. californica Cham. & Schlecht, Linnaea 2:35. 1827. *R. myriantha* Carr. Hort. Rev. 448. 1865. *R. californica* Cham. & Schlecht, var. *glandulosa* Crepin. Bull. Soc. Bot. Belg. 15:52. 1876. *R. californica* Cham. & Schlecht, var. *pubescens* Crepin. Bull. Soc. Bot. Belg. 15:52, 1876. *R. Aldersonii* Greene, Pittonia 5:110. 1903. *R. breweri* Greene, Leaflets Bot. Obs. & Crit. 2:262. 1912. *R. greenei* Rydb. Bull. Torr. Bot. Club. 44:71. 1917. *R. brachycarpa* Rydb. Bull. Torr. Bot. Club. 44:71. 1917. *R. santae-crucis* Rydb. Bull. Torr. Bot. Club. 44:73. 1917. *R. davyi* Rydb. Bull. Torr. Bot. Club. 44:76. 1917. *R. pilifera* Rydb. Bull. Torr. Bot. Club. 44:80. 1917. *R. johnstonii* Rydb. N. Am. Fl. 22:521. 1918.

Erect, branching shrub 1 to 3 m high; stem armed with stout, flattened, usually recurved prickles; floral branches armed with a pair of infrastipular prickles; stipules narrow, with lanceolate tips, often glandular-denticulate on the margins, usually pubescent; petiole and rachis pubescent, prickly, non-glandular to markedly glandular; leaflets 5 to 7, oval, rounded at both ends or acute at the apices, 1 to 3.5 cm long, the margins simply or doubly serrate, if double-toothed, the teeth gland-tipped, puberulent on the upper surface, pubescent and often glandular on the lower surface; flowers in corymbs subtended by leafy bracts; pedicels glabrous or villous, sometimes glandular; hypanthium glabrous or pilose when young, 10 to 15 mm thick, 8 to 16 mm long in fruit, globose or ovoid, usually with distinct neck; sepals lanceolate, caudate-attenuate, glabrous or pubescent on the backs, sometimes glandular; petals obcordate, 1 to 2.5 mm long; styles rarely exserted.

Common in moist places, along rivers, streams, and creeks, and near springs in the Coast Ranges and Sierra Nevada below 6,000 feet. California in the Coast Ranges from Humboldt County to the Laguna Mountains of San Diego County; in the Sierra San Pedro Martir of Baja California; in the Sierra Nevada from Butte County to Tulare County; on Santa Rosa, Santa Cruz, and Santa Catalina islands off the coast of California.

This is an extremely complex and variable population. Segregates have been proposed by various authors. These are based upon the following: size and shape of the leaflets; amount of indument on the surface of the leaflets; toothing of the leaflets, whether simply or doubly serrate and whether the teeth are gland-tipped or not; type of prickles, whether straight or recurved, stout or slender, numerous or few; shape of the hypanthium, whether pilose or glandular; and on the exsertion of the styles.

The following are examples of supposed entities which previously have been segregated out of the greater population. They are based upon characters not sufficiently consistent to warrant recognition of species. The plants do not form natural populations, but belong to a large polymorphic group, *R. californica.* A form named and described by Carriere (1865) as *R. myri-*

antha was segregated on the basis of its broadly oval leaflets, straight prickles, and depressed globose hypanthium (with no neck).

CALIFORNIA. MARIN CO.: Rodeo Lagoon, *K. Brandegee* in 1905 (UC). HUMBOLDT CO.: northwest of the junction of Willow Creek and Trinity River, *J. P. Tracy* 3410 (UC, US).

Greene (1903) split off a glandular form with doubly serrate leaflets. This he called *R. aldersonii*.

CALIFORNIA. SANTA BARBARA CO.: south of Lompoc, *W. N. Suksdorf* 185 (GH, WSC). SAN BERNARDINO CO.: road between Redlands and Yucaipa, *I. M. Johnston* 2120 (DS, POM, UC). SAN DIEGO CO.: below Cuyamaca Lake, *I. L. Wiggins* 2125 (DS); hills above Lake Henshaw, *D. Cole* 345, 348, 349. BAJA CALIFORNIA. Canyon of Rio Santo Domingo 6 miles above Mission, *I. L. Wiggins & D. Demaree* 4809 (DS, POM, UC, US). SANTA CRUZ ISLAND. Prisoners Harbor, *I. W. Clokey* 5190 (Cl-UC, GH, US, UTC, WASH).

Rydberg (1917) described several minor forms as species. He segregated *R. brachycarpa* on the basis of a hypanthium without a neck and of exserted styles. *R. greenei* was described as having an ellipsoid hypanthium with a long neck, and narrow elliptic leaflets.

(*R. brachycarpa*).—CALIFORNIA. SAN DIEGO CO.: Pacific Beach, San Diego, *M. Snyder* in 1900 (UC). RIVERSIDE CO.: Temescal Canyon, *I. M. Johnston* 1992 (DS, POM), *P. A. Munz* 7162 (POM). (*R. greenei*).—CALIFORNIA. MONTEREY CO.: Santa Lucia Mts., southwest of King City, *A. Simontacchi* 626 (UC). SANTA CLARA CO.: Block Mt., *W. R. Dudley* in 1894 (DS).

The characters upon which these entities are based are found in some individuals throughout the population, and they do not hold in combination in such a way as to form distinct entities.

SIGNIFICANT AND REPRESENTATIVE SPECIMENS

Number of specimens examined: 650.

CALIFORNIA. HUMBOLDT CO.: Willow Creek, *L. R. Abrams* 7161 (DS); Trinity River near south fork, *J. P. Tracy* 6550 (POM). TRINITY CO.: summit Scott Mts., north of Carville, *J. T. Howell* 12740 (CAS). MENDOCINO CO.: Arroyo Seco River, Santa Lucia Mts., *J. T. Howell* 5699A (DS); Russian River, 3 miles north of Ukiah, *L. R. Abrams* 8112 (DS). COLUSA CO.: Sycamore Slough, Stinchfield Ranch, *R. Stinchfield* 384 (DS, US, WILLU). BUTTE CO.: Berry Canyon near Clear Creek, *A. A. Heller & H. E. Brown* in 1902 (DS, GH, POM, US). MARIN CO.: Tomales Bay, *L. F. Henderson* 15583 (UO); Pt. Reyes, *A. Eastwood* 11777 (CAS). SONOMA CO.: Santa Rosa, *A. A. Heller* 5678 (DS, GH, POM, US); 2 miles north of Windsor, *A. Eastwood & J. T. Howell* 2523 (CAS). LAKE CO.: Eel River 1 mile below Hullville, *A. A. Heller* 6044 (DS, GH, POM, US); Kelseyville, *L. Benson* 10380 (POM). NAPA CO.: Napa River south of Napa, *W. N. Suksdorf* 636 (GH, WSC); Calistoga, *K. E. Phelps* in 1932 (CAS). SOLANO CO.: Collinsville, *J. T. Howell* 11691 (CAS); Alamo Creek, *W. L. Jepson* in 1891 (US). SACRAMENTO CO.: Sacramento, *G. Bentley* in 1923 (DS). AMADOR CO.: Ione, Mule Creek, *E. Braunton* 1090 (DS). CALAVERAS CO.: Calaveras Dam, *H. E. McMinn* 112 (DS). SAN MATEO CO.: Halfmoon Bay Road, *A. A. Heller* 8582 (DS, GH, UC, US, WASH); 2 miles back of Stanford Univ., *C. B. Wolf* in 1931 (UC). SANTA CRUZ CO.: Santa Cruz, *W. R. Dudley* in 1893 (DS); Corralitos, *W. W. Akey* 167 (VTM). SANTA CLARA CO.: Black Mt., *A. D. E. Elmer* 4284, (CAS, DS, OSC, POM, UC, UO, US, WSC); Los Altos, *M. Campbell* in 1918 (CAS, Cl-UC, US). ALAMEDA CO.: Berkeley Hills, *H. F. Copeland* in 1927 (UC). CONTRA COSTA CO.: Mitchell Canyon, Mt. Diablo, *M. L. Bowerman* 3545 (UC), *A. Carter* 1450 (UC). SAN JOAQUIN CO.: Stockton, *E. E. Stanford* 61 (DS); San Joaquin River near Lathrop, *W. N. Suksdorf* in 1913 (GH, WSC). TUOLUMNE CO.: Rawhide by Bear Creek, *Mrs. W. J. Williamson* 156 (CAS, Cl-UC, DS, POM), *R. Stinchfield* 25 (DS). MONTEREY

CO.: Carmel Bay, *A. D. E. Elmer* 4101 (DS, POM); Monterey, *S. B. Parish* 11601, (UC); Santa Lucia Mts., *J. T. Howell* 5658 (CAS). SAN BENITO CO.: San Juan Bautista, *D. Axelrod* 644 (VTM); Vancouver Pinnacles, *L. R. Abrams* 6715 (DS). MERCED CO.: eastern base of Pechecs Pass, *L. R. Abrams* 5304 (US); San Joaquin River east of Los Baños, *L. Benson* 7678 (POM). FRESNO CO.: Kings River east of Mendota, *W. R. Dudley* in 1903 (DS). TULARE CO.: Jack Ranch, Greenhorn Mts., *A. L. Cohen* 711 (POM). SAN LUIS OBISPO CO.: Adelaida, *G. T. Nordstrom* 1313 (VTM); Santa Inez Canyon, *J. H. Barber* in 1898 (UC). SANTA BARBARA CO.: Santa Barbara Canyon, *W. A. Peterson* 316 (UC); trail to Manzana Creek, Zaca Lake Forest Reserve, *A. Eastwood* 669 (CAS). VENTURA CO.: Red Reef Canyon, Topatopa Mts., *L. R. Abrams & E. A. McGregor* 135 (DS, GH, OSC, POM). LOS ANGELES CO.: Santa Monica Mts., *I. W. Clokley & B. Templeton* 4559 (Cl-UC, GH, POM, UC, US); Live Oak Canyon, Claremont, *H. P. Chandler* in 1897 (POM); Russels Lake, *L. R. Abrams* 5016 (DS); 2 miles northwest of Castaic Peak, *A. D. Gifford* 146 (VTM); north side of Griffith Park, *E. Braunton* 388, (US); Sepulveda Canyon, Santa Monica Mts., *L. R. Abrams* 2539 (DS, GH, POM, UC, UO, US); Kings Canyon, Liebre Mts., *W. R. Dudley & F. H. Lamb* 4396 (DS, US). ORANGE CO.: Santa Ana Canyon, *J. T. Howell* 2445 (CAS); Newport Lagoon, *L. M. Booth* 1161 (POM); Laguna Canyon, San Joaquin Hills, *I. M. Johnston* 2140 (DS, POM, UC); Laguna, *L. Schoenefeldt* in 1894 (US). SAN BERNARDINO CO.: Bear Valley, San Bernardino Mts., *S. B. Parish* 3387 (US); Cucamonga Canyon, *I. M. Johnston* 1590 (DS, POM, UC); San Bernardino, *S. B. Parish* 4191 (GH, US). RIVERSIDE CO.: 15 miles south of Hemet, *P. A. Munz* 10887 (POM); Riverside, *H. M. Hall* 588 (UC). SAN DIEGO CO.: Palomar Mt., *M. E. Jones* in 1926 (POM); Descanso, *A. Eastwood* 9081 (CAS); Cuyamaca, *A. S. Hitchcock* in 1915 (US); Barrett Dam, *P. A. Munz* 7982 (POM); Oceanside, *E. Merrill* in 1923 (POM); Julian, *E. A. M:Gregor* in 1918 (DS); brookside near San Diego, *M. F. Spencer* 140 (UC, US). SANTA CRUZ ISLAND: Willow Harbor, *M. W. Williams* 73 (DS), 74 (POM); Ravenwood, *J. T. Howell* 6233 (CAS); between Main Ranch and Prisoners Harbor, *C. B. Wolf* 4132 (DS, UC, US). SANTA ROSA ISLAND: along stream outer side of island, *P. A. Munz* 11721 (GH, POM); Water Canyon, 1.5 miles inland, *R. Hoffman* 109 (POM). SANTA CATALINA ISLAND: Avalon, *B.. Trask* in 1895 (US); Middle Ranch Canyon, *M. B. Dunkle* 1946 (POM), *J. Giddings* in 1924 (DS).

BAJA CALIFORNIA. La Encantada Sierra San Pedro Martir, *I. L. Wiggins & D. Demaree* 4916 (CAS, DS, POM, UC, US); La Grulla, *E. A. Goldman* 1254 (US); 15 miles northeast of Ojos Negros on road to Neji Rancho, *I. L. Wiggins & Gillespie* 4118, (CAS, DS, POM); San Ysidro Ranch, *E. A. Mearns* in 1894 (DS, US).

Type collections: (1) *R. aldersonii*, "collected on Witch Creek, San Diego Co., California, in June 1894, by R. D. Alderson." Type probably in Herbarium Greeneanum at the University of Notre Dame; Isotype (DS 96987), photograph (POM). (2) *R. brewerii*, "collected on the Calif. Geol. Survey 50 years since, by W. H. Brewer, near San Jose, August 30 in very ripe fruit." Type (US 320924), photograph (POM). (3) *R. greenei*, "California: Santa Cruz Island, July and August 1886, E. L. Greene." Type (US 45935), photograph (POM). (4) *R. brachycarpa*, "Temescal Canon, near Elsinore, May 23, 1892, *McClatchie*." Type (NY) (no number), photograph (POM). (5) *R. santae-crucis*, "island of Santa Cruz, 1886, E. L. Greene." Type probably in Herbarium Greeneanum at the University of Notre Dame. (6) *R. davyi*, "Saratoga, Davy 263." Type in Herbarium of Columbia University (no number), photograph (POM). (7) *R. pilifera*, "California, San Francisco, Dr. Bolander"; (no date given). Type in Herbarium of Columbia University (no number), photograph (POM). (8) *R. johnstonii*, "Type collected near Upland, San Bernardino County, California July 4 and August 24, 1918, I. M. Johnston 2050 (in flower) and 2130 (in fruit)." Isotype (NY) (no number), photograph (POM).

3. ROSA PINETORUM Heller.

R. pinetorum Heller, Muhlenbergia, 1:53. 1904. *R. bolanderi* Greene, Leaflets Bot. Obs. & Crit. 2:261. 1912. *R. calvaria* Greene, loc. cit. 257. *R. dudleyi* Rydb. Bull. Torr. Bot. Club. 44.73. 1917. *R. bidenticulata* Rydb. N. Am. Fl. 22:518. 1918. *R. corymbiflora* Rydb. loc. cit. 519. *R. gymnocarpa* Nutt. var. *pinetorum* (Hel.) Jeps. Man. Fl. Pl.

Calif. 500. 1925. *R. californica* var. *bidenticulata* (Rydb.) Erlanson, Bot. Gaz. 96:222. 1934.

Erect shrub, 5 to 10 dm high; stem densely armed with straight, slender, weak prickles, the infrastipular prickles stouter and longer; floral branches prickly with stout, straight infrastipular prickles 1 cm long, or sometimes unarmed; stipules pubescent and often glandular on the upper surfaces, the margins glandular-ciliate; petiole and rachis pubescent, glandular-hispid, prickly; leaflets usually 5, elliptic to broadly oval, rounded at the bases and apices, puberulent beneath and glandular, the margins doubly serrate with gland-tipped teeth, 2 to 3 cm long, the midribs prominent; flowers usually solitary or in few-flowered corymbs; pedicels glandular-hispid; hypanthium globose, glabrous, 6 to 12 mm thick, 7 to 14 mm long in fruit; sepals glandular on the backs, sometimes glabrous, with foliaceous tips, persistent in fruit.

In open or shady pine forests, Transition Zone. California; Humboldt Co. to Monterey Co.; Sierra Nevada; from Shasta Co. to Tulare Co.

SIGNIFICANT AND REPRESENTATIVE SPECIMENS

Number of specimens examined: 55.

CALIFORNIA. HUMBOLDT CO.: Clam Beach, Trinidad, *L. Benson* 442 (POM); Table Bluff, *I. L. Wiggins* 9488 (DS, GH). SAN MATEO CO.: mouth of Waddell Creek, *H. L. Mason* 4128 (UC). SANTA CRUZ CO.: Santa Cruz, *C. H. Thompson* in 1903 (DS). SANTA CLARA CO.: near Saratoga, *R. L. Pendleton* 396 (UC); Guadalupi Creek above San Jose, *W. R. Dudley* 1893 (DS). MONTEREY CO.: Monterey, *G. Englemann* in 1880 (GH); Point Lobos, *A. Eastwood & J. T. Howell* 6036 (CAS, POM, US); Pacific Grove, *L. E. Cox* in 1908 (DS); Point Pinos Lighthouse, *A. A. Heller* 8413 (CAS, DS, GH, US). EL DORADO CO.: 3 miles east of Camino, *G. T. Robbins* 1652 (CAS, GH). TULARE CO.: Kaweah River Valley, *W. R. Dudley* 1313a (DS); Alta Peak, Sequoia Natl. Park, *W. R. Dudley* 1642 (DS).

Type collections: (1) *R. pinetorum*, "Collected in sandy pine woods about Pacific Grove, Monterey county, California, June 3, 1903." *A. A. Heller* 6817. Isotypes (DS, GH, NY, POM, US), photograph (POM). (2) *R. bolanderi*, "Known only as collected by H. N. Bolander, at some unrecorded station among the Oakland Hills."(No date given). Type (US 45934), photograph (POM). (3) *R. calvaria*, "Collected by writer, at the Calaveras Big Tree Grove in June, 1889." Type probably at Herbarium Greeneanum at the University of Notre Dame (HGR 11192). (4) *R. dudleyi*, CALIFORNIA. FRESNO CO.: near Booles Home, Converse Basin, *W. R. Dudley* 3388. Isotypes (DS, GH, US), photograph (POM). (5) *R. bidenticulata*, "Collected at Castella, Shasta Co., California, July 24, 1912, *Alice Eastwood* 1389." Type probably at Arnold Arboretum Herb., Harvard Univ.; Isotype (CAS), photograph (POM). (6) *R. corymbiflora*, "collected in Shasta County, California, between Pitt and Baird, July 25, 1912, *Alice Eastwood* 1404." Type probably at Arnold Arboretum Herb., Harvard Univ.; Isotype (CAS), photograph (POM).

4. ROSA PISOCARPA A. Gray

R. pisocarpa A. Gray, Proc. Amer. Acad. 8:382. 1872. *R. rivalis* Eastw. Bull. Torr. Bot. Club. 32:198. 1905. *R. pringlei* Rydb. Bull. Torr. Bot. Club. 44:79. 1917. *R. eastwoodiae* Rydb. N. Amer. Fl. 22:527. 1918. *R. pisocarpa* A. Gray, var. *rivalis* (Eastw.) Jeps. Man. Fl. Pl. Calif. 499. 1925.

Slender shrub, 1 to 2 m high; stems slender with dark brown bark, armed with few slender, straight, frequently ascending infrastipular prickles; floral branches armed with straight or ascending infrastipular prickles or unarmed; stipules narrow, dilated upwards, sometimes slightly glandular on the margins; petiole and rachis pubescent, sometimes prickly; leaflets usually 7, oval or oblong-ovate, rounded at the bases, the margins simply and finely serrate, glabrous above, pubescent or sometimes glabrous below, the veins standing out on the lower surfaces of the leaflets; flowers corymbose or solitary, subtended by leaf-like bracts; hypanthium smooth, globose, 7 to 10 mm thick, 5 to 11 mm long in fruit; pedicel glabrous; sepals lanceolate, caudate-attenuate, glandular-hispid on the backs; petals obcordate, 8 to 15 mm long.

Humid regions on rich hillsides and slopes; sometimes in thickets; Transition Zone. Vancouver Island and the mainland of British Columbia; Washington west of the Cascades and in western Klickitat County; Oregon west of the Cascades to northern Lake County, California, and eastward to Siskiyou County.

SIGNIFICANT AND REPRESENTATIVE SPECIMENS

Number of specimens examined: 350.

BRITISH COLUMBIA. VANCOUVER ISLAND: near Victoria, *J. Macoun* in 1893 (GH), *Fletcher* in 1885 (GH); Mt. Tolmie, *J. G. Jack* 2855 (CAS); Quanichau, *W. R. Carter* in 1917 (US). MAINLAND: Huntingdon, *T. T. McCabe* 3716 (UC); Fort Steele, *W. B. Anderson* 2074 (WSC); Oak Bay, Nanaimo, *J. R. Anderson* in 1917 (WSC).

WASHINGTON. WHATCOM CO.: Samish Lake, *W. N. Suksdorf* in 1890 (WSC); Bellingham Bay, *W. N. Suksdorf* in 1890 (WSC). SNOHOMISH CO.: Snohomish River, *G. N. Jones* 4954 (CAS, POM, WASH); Everett, *G. N. Jones* 4895 (GH, WASH). JEFFERSON CO.: Brinnon, *R. K. Beattie* 3087 (Cl-UC). KING CO.: Seattle, *C. V. Piper* in 1896 (US, WASH), *J. W. Thompson* 5205 (DS, GH, WASH); 6 miles southeast of Auburn, *A. Eastwood & J. T. Howell* 2886 (CAS). GRAYS HARBOR CO.: near Satsop, *A. A. & E. G. Heller* 4032 (GH, POM, UC, US, WSC). MASON CO.: 1.8 miles north of Hoodsport, *G. N. Jones* 8697 (GH, WASH). KITSAP CO.: along beach, Waterman, *F. A. Warren* 94 (WSC). THURSTON CO.: Grand Mound, *G. N. Jones* 142 (WASH). PIERCE CO.: near Buckley, *P. Eide* in 1930 (WSC). WAHKIAKUM CO.: Altoona, *W. N. Suksdorf* 6810 (WSC). COWLITZ CO.: near Long-bell Ferry, Longview, *L. R. Abrams* 9300 (DS). CLARK CO.: Lacamas Creek, *C. English Jr.* 1131 (WSC). KLICKITAT CO.: Falcon Valley, *W. N. Suksdorf* 7878 (WSC), 7293 (WSC); falls, White Salmon River, *W. N. Suksdorf* in 1899 (WSC).

OREGON. MULTNOMAH CO.: Willamette River below Portland, *E. P. Sheldon* in 1902 (Cl-UC, DS, GH, POM, UO, WSC). WASCO CO.: Warm Spring River, *E. I. Applegate* 2776 (US). CLACKAMAS CO.: Milwaukee, *W. N. Suksdorf* in 1893 (WSC); Willamette Falls, *E. P. Sheldon* in 1902 (UO). MARION CO.: 2 miles south of Salem, *L. R. Abrams* 8758 (DS, POM); Macleary, *F. V. Coville* 837 (US). LINCOLN CO.: Devils Lake, *L. F. Henderson* 11745 (UO). LINN CO.: Calapooya-Santiam Divide, *L. F. Henderson* 13720 (UO). LANE CO.: Cottage Grove, *M. E. Peck* 6613 (WILLU); Cresswell, *L. R. Abrams* 8712 (DS, POM, UO, WILLU). COOS CO.: Marshfield, *H. D. House* 4796 (US). DOUGLAS CO.: North Fork of Umpqua River, *E. I. Applegate* 2725 (US); Glendale, *M. E. Peck* 6603 (WILLU). CURRY CO.: Harbor, *M. E. Peck* 8727 (GH, WILLU); banks of Chetco River, *L. F. Henderson* 11746 (UO). JOSEPHINE CO.: foot of Sexton Mt., *M. E. Peck* 16346 (WILLU); Grants Pass, *M. E. Peck* 2161 (WILLU). JACKSON CO.: Natural Bridge of the Rogue, *J. W. Thompson* 12328 (WASH, WILLU); Ashland, *E. I. Applegate* 2189 (US).

CALIFORNIA. DEL NORTE CO.: Gasquet, *J. P. Tracy* 12721 (UC); Smith River near Adams, *A. Eastwood* 12248 (CAS). SISKIYOU CO.: Happy Camp to Waldo Road, *E. Lee* 1123 (UC), *A. Carter* 704 (DS, UC). HUMBOLDT CO.: Grouse Mt., *J. P. Tracy* 12898 (GH, UC, WASH), 13416 (UC); Klamath River, *H. P. Chandler* (GH, UC, US). TRINITY CO.: Hettensh-w Valley, *J. P. Tracy* 16946 (GH, UC, US); Cartville, *J. T. Howell* 14857 (CAS). MENDOCINO CO.: Laytonville, *A. Eastwood* 9361 (DS), 9362 (CAS, GH, US); 1 mile south of Longvale, *D. K. Kildale* 3512 (DS). LAKE CO.: Elk Mt., *J. P. Tracy* 2305 (UC).

Type collections: (1) *R. pisocarpa*, Originally described by Gray in Proc. Amer. Acad. 8:382, in 1872 as "Rather doubtfully distinguished from forms of *R. californica* by the somewhat smaller and more globose fruit, and by the spines never recurved but very frequently ascending." (2) *R. rivalis*, "collected by author along small stream, in the shade of the trees, near Laytonville, Mendocino County, California, August 3, 1902." (3) *R. pringlei*, CALIFORNIA. SISKIYOU CO.: by streams, *C. G. Pringle* in 1882. Type (NY) (no number), photograph (POM); Isotype (US). (4) *R. eastwoodiae*, "collected at Sisson, Siskiyou Co., California, September 4, 1912, *Alice Eastwood* 2100." Type probably in Arnold Arboretum Herb.; Isotype (CAS), photograph (POM).

5. ROSA WOODSII Lindl.

Erect, stout shrub 1 to 3 m high; stem armed (sometimes densely so) with straight, slender, stramineous prickles; floral branches often unarmed or, if armed, with a pair of straight, slender infrastipular prickles; stipules pubescent below and on the margins or sometimes entirely glabrous, glandular-ciliate or glandular-dentate, sometimes glandular-pruinose below, lower stipules narrow, the upper often dilated; petiole and rachis pubescent or glabrous, glandular-pruinose, rarely prickly, sometimes quite reddish; leaflets 5 to 7, oval, rounded at both ends, sometimes cuneate at the bases, glabrous above, pubescent or glabrous below, often glandular-pruinose below, the margins simply, sharply, and coarsely serrate, 1 to 4 cm long; flowers in corymbs or solitary, subtended by leaf-like bracts; pedicels glabrous; hypanthium glabrous, ellipsoid to globose, 7 to 10 mm thick, 5 to 12 mm long in fruit; sepals glabrous on the backs, entire, rarely glandular, caudate-attenuate; petals obcordate 1.5 to 2 cm long.

5a ROSA WOODSII Lindl. var. ULTRAMONTANA (S. Wats.) Jeps.

R. californica Cham. & Schlecht, var. *ultramontana* S. Wats. Bot. Calif. 1:187. 1876. *R. ultramontana* (S. Wats.) Heller, Muhlenbergia 1:107. 1904. *R. puberulenta* Rydb. Fl. Rocky Mts. 443. 1917. *R. pyrifera* Rydb. loc. cit. 445. *R. salictorum* Rydb. Bull. Torr. Bot. Club. 44:77. 1917. *R. chrysocarpa* Rydb. loc. cit. 74. *R. rotundata* Rydb. loc. cit. 76. *R. Woodsii* Lindl. var. *ultramontana* (S. Wats.) Jeps. Fl. Calif. 2:210. 1936. *R. lapwaiensis* St. John, Fl. S. E. Wash. and Adj. Idaho 208. 1937. *R. pisocarpa* A. Gray, var. *ultramontana* (S. Wats.) Peck, Man. Higher Pl. Oregon. 404 (as *transmontana*) errata. 1941. Cf. table I.

In arid regions East of the Cascade Mountains and the Sierra Nevada. British Columbia; south through eastern Washington and Oregon; into Idaho and northwestern Montana; California along Eastern slope of the Sierra Nevada; Nevada and western Utah.

This group is variable. Erlanson (1929) described it as the "diploid group" of the Great Basin Region. She placed all of the plants of this area under one species, *R. woodsii*. Rydberg (1917a, 1917b) segregated out several of the variants as species. The following are examples:

R. puberulenta was differentiated on the basis of bristly young shoots and dorsally puberulent sepals. The following specimens are examples of *R. puberulenta:*

OREGON. GRANT CO.: Dayville, *H. L. Mason* 3583 (UC). WALLOWA CO.: near Wallowa, *A. W. Sampson & G. A. Pearson* 78 (US).

R. pyrifera was distinguished by the stalked hypanthium and glandular sepals. Examples:

WASHINGTON. WHITMAN CO.: Pullman, *C. V. Piper* in 1896 (GH). OREGON. DOUGLAS CO.: Thompson Creek, foot of Buck Mt., *W. I. Brown* 86 (US). NEVADA. ELKO CO.: west end of Harrison Pass, *A. A. Heller* 9459 (US).

R. salictorum was segregated out on the basis of large, thin, broadly oval leaflets, few and slender prickles, few prickles except on new shoots. Examples:

NEVADA. ELKO CO.: Star canyon, southeast of Deeth, *A. A. Heller* 10570 (DS, GH, US). LANDER CO.: Toiyabe Range, *P. B. Kennedy* 4106 (DS).

SIGNIFICANT AND REPRESENTATIVE SPECIMENS

Number of specimens examined: 725.

BRITISH COLUMBIA. Near stream, Lower Nicola, *C. V. Copley* 7840 (WSC); Spence's Bridge, *J. R. Anderson* 551 (WSC); near the International Boundary between the Kettle and Columbia rivers, *J. Macoun* 65009 (WSC).

WASHINGTON. CHELAN CO.: Ingalls Creek, *J. W. Thompson* 10557 (GH); Pesh-

astin, *L. Benson* 2455 (DS, POM, US). DOUGLAS CO.: Junction of Crab and Wilson Creeks, *J. H. Sandberg & J. B. Leiberg* 320 (GH, UC, US, WSC). FERRY CO.: 10 miles below Republic, *R. Sprague* 372 (WSC). STEVENS CO.: Columbia River 10 miles south of Northport, *C. W. Sharsmith* 4039 (CAS, DS, GH, UC, WASH, WSC). LINCOLN CO.: Columbia River 3 miles above Grand Coulee Dam, *H. T. Rogers* 466 (CAS, Cl-CU, DS, GH, POM, US, WASH, WSC). SPOKANE CO.: Cheney, *W. N. Suksdorf* in 1889 (WSC). KITTITAS CO.: Swauk, Wenatchee Range, *L. Benson* 5518 (POM); Ellensberg, *G. N. Jones* 1406 (WASH), *K. Whited* 677 (OSC, UO, US, WSC). GRANT CO.: southwest of Moses Lake, *St. John, Courtney, & Parker* 4928 (GH, UC, WASH, WSC). ADAMS CO.: 2 miles northeast of McCall, *R. G. Jeffrey* in 1946 (WSC). WHITMAN CO.: Pullman, *C. V. Piper* 1538 (GH, US, WSC), *G. N. Jones* 1950 (WASH). YAKIMA CO.: Yakima, *G. N. Jones* 1421 (WASH). KLICKITAT CO.:

TABLE 1.—Varieties of *Rosa woodsii*.

	var. *ultramontana*	var. *gratissima*	var. *glabrata*
Habit	erect, 1-3 m high, stout	branched, 1-2 m high	slender, 5-10 dm high
Stem	armed with straight, slender prickles	densely armed with straight slender, stramineous prickles; longer and stouter prickles infrastipular	well-armed, prickles scattered
Floral branches	long, often unarmed, if armed, with a pair of straight, slender, stramineous, infrastipular prickles	long, usually heavily armed	short, armed with straight frequently descending prickles
Stipules	pubescent below and on the margins, glandular-ciliate or glandular-dentate, sometimes glandular pruinose below; lower stipules narrow, the upper dilated	pubescent below, broad, the margins entire or dentate, sometimes not glandular	glabrous, usually entire non-glandular except on the margins; upper stipules not dilated
Petiole & rachis	pubescent, glandular-pruinose, rarely prickly, sometimes reddish.	pubescent, glandular, prickly	glabrous, somewhat prickly
Leaflets	5 to 7, pubescent below and often pruinose, firm, 1 to 4 cm long	5 to 7, sometimes pubescent below, thin, 1 to 2 cm long	3 to 5, glabrous, shiny above, 0.5 to 1.5 cm long
Flowers	in corymbs	solitary or in corymbs	usually solitary
Pedicel	glabrous	usually glabrous	glabrous
Hypanthium	glabrous, ellipsoid to globose, 7 to 10 mm wide at maturity, 7 to 12 mm long	glabrous, globose, about 8 mm wide at maturity, 6 to 10 mm long	glabrous, globose to ovoid, 7 to 10 mm thick, 5 to 12 mm long
Sepals	entire, caudate-attenuate, rarely glandular	sometimes glandular	non-glandular
Petals	1.5 to 2 cm long	1.5 cm long	1 to 1.5 cm long

bottomlands, Bingen, *W. N. Suksdorf* in 1898 (WSC). BENTON CO.: Prosser, *J. S. Cotton* 1093 (WSC). WALLA WALLA CO.: Walla Walla, *G. A. Hill* in 1911 (WSC). COLUMBIA CO.: Blue Mts., *Lake & Hull* 819 (WSC), *C. V. Piper* in 1896 (GH). ASOTIN CO.: bank of the Snake River 3 miles south of Asotin, *C. L. Hitchcock & C. V. Muhlick* 8368 (DS, GH, WASH, WSC).

OREGON. WASCO CO.: bank of Deschutes River near Maupin, *M. E. Peck* 17346 (WILLU). SHERMAN CO.: near the mouth of John Day River, *L. F. Henderson* 5467 (CAS, DS). UMATILLA CO.: 20 miles northeast of Pendleton, *M. E. Peck* 18091 (WILLU). UNION CO.: Blue Mts., *W. C. Cusick* 1705 (DS, GH). WALLOWA CO.: northeast end of Wallowa Lake, *L. Constance & A. D. Jacobs* 1292 (CAS, WASH, WSC). JEFFERSON CO.: open woods, Camp Sherman, *M. E. Peck* 19757 (WILLU). CROOK CO.: Pineville, *J. B. Leiberg* 838 (GH). DESCHUTES CO.: near Lava Butte, *J. T. Howell* 7042 (CAS). KLAMATH CO.: Swan Lake Valley, *E. I. Applegate* 3639 (DS); Yainax Valley, *F. V. Coville* 1318 (US). LAKE CO.: south of Summer Lake, *M. E. Peck* 15680 (WILLU). HARNEY CO.: Willow Creek Canyon, *M. E. Peck* 19028 (WILLU); Alvord Ranch, *L. F. Henderson* 9088 (CAS). MALHEUR CO.: Owyhee Canyon, *M. E. Peck* 21244 (WILLU).

CALIFORNIA. MODOC CO.: Willow Ranch, *E. I. Applegate* 5904 (UC). SHASTA CO.: south of Bieber, *E. I. Applegate* 5876 (DS, GH, UC). LASSEN CO.: Vickers, *M. S. Baker* in 1898 (UC). PLUMAS CO.: 3 miles north of Hawks, *E. Sawyer* 171 (UC, VTM). SIERRA CO.: Sierraville, *G. T. Nordstrom* 930 (VTM). PLACER CO.: Truckee River, *C. F. Sonne* 86 (DS). EL DORADO CO.: 6 to 8 miles southeast of Lake Tahoe, *G. T. Robbins* 2146 (CAS, UC). NEVADA CO.: lower end of Donner Lake, *A. A. Heller* in 1903 (US). ALPINE CO.: east side of Ebbetts Pass, *A. Eastwood & J. T. Howell* 8495 (CAS). MONO CO.: Convict Lake, *J. T. Howell* 14440 (WASH); Bridgeport, *T. M. Hendrix* 470 (UC, VTM). INYO CO.: Bishop, *E. Larsen* in 1925, (CAS).

IDAHO. NEZ PERCE CO.: near Lewiston, *A. A. Heller & E. G. Heller* 3141 (DS, UC, US, WASH). IDAHO CO.: 7 Devils Mts., *J. Packard* 266 (UC, WSC). LEMHI CO.: near Salmon River 20 miles south of Gibbonville, *C. L. Hitchcock & C. V. Muhlick* 9040 (CAS, DS, GH, WASH, WSC). CUSTER CO.: Clayton, *J. H. Christ* 11377 (UC). BOISE CO.: Sweet, *J. F. McBride* 1620 (DS, GH, WSC). CANYON CO.: New Plymouth, *J. F. McBride* 180 (GH, US, WSC). ADA CO.: 15 miles from Boise on the road to Idaho City, *F. A. McFadden* 15755 (CAS). ELMORE CO.: North Fork Boise River, 3 miles west of Deer Park Lodge, *C. L. Hitchcock & C. V. Muhlick* 10066 (WASH, WSC). BLAINE CO.: 4 miles north of Hailey along Wood River, *C. L. Hitchcock & C. V. Muhlick* 10434 (CAS, DS, GH, WSC). TWIN FALLS CO.: Twin Falls, *J. F. McBride* 1322 (DS, GH, POM, UC). MADISON CO.: Salem, *R. J. Davis* 233 (DS, UC, WSC).

MONTANA. MINERAL CO.: Lee Creek Camp, Lola Hot Springs, *C. L. Hitchcock & C. V. Muhlick* 14619 (WASH). RAVILLI CO.: 15 miles west of summit of Skalkado Road, *C. L. Hitchcock & C. V. Muhlick* 14510 (UC, WASH, WSC). MISSOULA CO.: Missoula, *M. E. Jones* in 1909 (POM, UC). GRANITE CO.: Rock Creek Canyon, *C. L. Hitchcock & C. V. Muhlick* 14407 (WASH, WSC). FLATHEAD CO.: Columbia Falls, *R. S. Williams* 965 (US); Bigfork, *M. E. Jones* in 1908 (CAS, DS, POM, US). GLACIER CO.: Going-to-the-Sun-Chalets, on St. Mary Lake, *P. C. Stanley* 17320 (US).

NEVADA. WASHOE CO.: mountains west of Franktown, *A. A. Heller* 10519 (CAS, DS, GH, POM, US); Pyramid Lake, *N. D. Kennedy* 1007 (DS); Riverside Park, Reno, *A. A. Heller* 9978 (DS, GH, US). HUMBOLDT CO.: Summit Lake Creek, *P. Train* 3020 (Cl-UC, WASH). ELKO CO.: Lamoille, *A. H. Holmgren* 1924 (UC); South Fork of the Humboldt, *A. A. Heller* 9430 (US). ORMSBY CO.: Kings Grade, Carson City, *L. Benson* 6706 (POM), *C. F. Baker* 1221 (CAS, GH, UC). DOUGLAS CO.: Wellington, *T. M. Hendrix* 1096 (VTM). STOREY CO.: 1 mile southeast of Virginia City, *R. A. Allen* 158 (WASH). ESMERALDA CO.: 1 mile west of Lida Summit, Mt. Magruder, *A. M. Alexander & L. Kellogg* 2451 (UC). NYE CO.: Kingston Canyon, Toiyabe Mts., *I. Tidestrom* 10942 (US).

Type collections: (1) *R. ultramontana*, Originally described as a variety of *R. californica* by Watson in Botany of California 1:187, in 1876 as "tomentose but not glandular; calyx tube and pedicels glabrous: prickles straight and slender." "the variety occurring

on the eastern side of the Sierra Nevada, ranging to the Rocky Mountains." (2) *R. puberulenta,* "Montezuma Canyon, east of Monticello, Utah." (3) *R. pyrifera,* "Shores of Lake Pend d' Oreille, Idaho." IDAHO. KOOTENAI CO.: Lake View, *J. H. Sandberg* 871. Isotype (US), photograph (POM). (4) *R. salictorum,* Described by Rydberg in Bull. Torrey Bot. Club 44:77, in 1917 as "Related to *R. pisocarpa* and *R. ultramontana,* but differs from both in the large thin, broadly, oval leaflets and the few slender prickles. It is almost unarmed except on the new shoots, it also differs from the former in the non-glandular sepals." NEVADA. Gold Creek, *Nelson & McBride* 2113. Type (NY), photograph (POM). (5) *R. chrysocarpa,* UTAH. Allen Canyon, southwest of Abajo Mts., *Rydberg & Garrett* 9302. Type (NY), photograph (POM). (6) *R. rotundata,* NEVADA. WASHOE CO.: mountains west of Franktown, *A. A. Heller* 10520. Type (NY), photograph (POM); Isotype (US). (7) *R. lapwaiensis,* IDAHO. NEZ PERCE CO.: flat by Lapwai Creek, Spaulding, *H. St. John* 9538. Type (WSC—two sheets), photograph (POM).

5b Rosa woodsii Lindl. var. gratissima (Greene) D. Cole, comb. nov.

R. gratissima Greene. Fl. Fran. 73. 1891. *R. pisocarpa* A. Gray. var. *gratissima* (Greene) Jeps. Man. Fl. Pl. Calif. 499. 1925. Cf. Table 1.

In the southern Sierra Nevada from Fresno and Mono counties to Kern and Inyo counties, California; yellow pine belt in Ventura, Los Angeles and San Bernardino counties; Nevada in Douglas and Esmeralda counties.

SIGNIFICANT AND REPRESENTATIVE SPECIMENS

Number of specimens examined: 175.

CALIFORNIA. FRESNO CO.: Pilot Knob, south side, under cliff, *R. L. Armacost* 82 (POM). TULARE CO.: Kern River Region, Granite Basin, *W. R. Dudley* 741 (DS); upper Tule River, near Nelson's, *W. R. Dudley* 2655 (DS); North Fork of the Kern River, *F. V. Coville & F. Funston* 1720 (DS, US). KERN CO.: Water Canyon, Tehachapi Mts., *L. R. Abrams & E. A. McGregor* 482 (DS, GH, US). VENTURA CO.: Griffins, Mt. Pinos, *A. D. E. Elmer* 3732 (DS, GH, POM, US). LOS ANGELES CO.: Prairie Fork of the San Gabriel River, *I. M. Johnston* 1704 (DS, POM, UC); Big Pines, Swartout Valley, *F. W. Peirson* in 1922 (POM). SAN BERNARDINO CO.: 2 miles east of Bluff Lake, San Bernardino Mts., *P. A. Munz* (POM). MONO CO.: Sherwin Grade, *J. T. Howell* 14373 (CAS). INYO CO.: Big Pine Creek, *R. S. Ferris* 9009 (DS, UC); Cottonwood Creek, *C. B. Wolf* 3256 (CAS, DS, GH, POM); Wild Rose Canyon, Panamint Mts., *J. T. Howell & A. Eastwood* 7842 (CAS); Stressi's Place, Death Valley, *M. F. Gilman* 3853 (POM); 5 miles south of Independence, *L. Benson* 5915 (POM).

NEVADA. DOUGLAS CO.: Glenbrook, near Lake Tahoe, *W. R. Dudley* in 1900 (DS). ESMERALDA CO.: Trail Canyon, White Mts., *V. Duran* 3089 (CAS, DS, POM, UC, US, WASH, WSC).

Type collections: (1) *R. gratissima,* "Borders of wet meadows, and about springy places in the mountains of Kern Co."

5c Rosa woodsii Lindl. var. glabrata (Parish) D. Cole, comb. nov.

R. californica Cham. & Schlecht, var. *glabrata* Parish, Erythea 6:88. 1898; not *R. glabrata* Kit in 1863. *R. mohavensis* Parish, Bull. So. Calif. Acad. Sci. 1:87. 1902. *R. woodsii* Lindl. var. *mohavensis* (Parish) Jeps. Fl. Calif. 2:210. 1936. Cf. Table 1.

Moist places in canyons; eastern slope of the San Bernardino Mountains at Box 'S' Springs and Cushenberry Springs, San Bernardino County, California.

SIGNIFICANT AND REPRESENTATIVE SPECIMENS

Number of specimens examined: 35.

CALIFORNIA. SAN BERNARDINO CO.: 1½ miles northeast of Rattlesnake Mt., San Bernardino Mts., *D. Axelrod* 369 (VTM); Box 'S' Springs, Mohave Desert, *H. L.*

Mason 3090 (GH, UC), *S. B. Parish* 19277 (GH, UC); Cushenberry Springs, *S. B. Parish* 4941 (DS, UC, US), *C. B. Wolf* in 1932 (CI-UC, WASH); 2 miles west of Cushenberry Springs, *P. A. Munz & F. Youngberg* 14962 (GH, POM); Cienega near Cushenberry Springs, *E. C. Jaeger* 954 (US); Whiskey Spring, Cushenberry Canyon, *M. E. Jones* in 1926 (POM).

Type collections: (1) var. *glabrata*, "on desert side of San Bernardino Mts., near water, Cushenberry Springs, alt. 4,000 ft., June 1, 1892, 2481 *Parish*." "Types in Hb. Gray & Hb. Parish." (2) *R. mohavensis*, Originally described as a variety (*glabrata*) of *R. californica* by Parish in Erythea. 6:88. 1898. Same entity based on same specimen raised to species rank by Parish in Bull. So. Calif. Acad. Sci. 1:87. 1902. "Type 2481 *Parish*, June 1, 1892, collected by water courses at Cushenberry Springs, at the desert foot of the San Bernardino Mts., alt. about 4,000 ft. Since received from Mr. H. M. Hall, who collected it in 1900 on the desert slope of San Antonio Mt. Also collected long ago at Rock Creek, in the same region, by Dr. Davidson, and probably not uncommon on the borders of the Mohave Desert."

REFERENCES

BRIQUET, JOHN 1935—International rules of Botanical Nomenclature. 117. New York Botanical Garden.

CARRIERE 1865—Revue Horticule. Librairie Agricole de la Maison Rustique, Paris.

ERLANSON, EILEEN W. 1929—Cytological Conditions and Evidences for Hybridity in North American Wild Roses. Bot. Gaz. 87:443-506.

——— 1934—Experimental data for a Revision of the North American Wild Roses. Ibid. 96:197-259.

——— 1938—Phylogeny and Polyploidy in Rosa. New Phytol. 37:72-81.

GREENE, E. L. 1903—New or Noteworthy Species. Pittonia 5:110.

——— 1912—Certain Western Roses. Leaflets of Botanical Observation & Criticism. 2:255-266.

JONES, GEORGE N. 1935—The Washington Species and Varieties of Rosa. Madroño 3:120-135.

LANJOUW 1952—International Rules of Botanical Nomenclature. New Code. See also BRIQUET.

LINDLEY, JOHN 1820—Rosarum Monographia. James Ridgeway, Piccadilly, London.

RYDBERG, PER AXEL 1917a—Notes of Rosaceae. Bull. Torr. Bot. Club. 44:65-84.

——— 1917b—The Flora of the Rocky Mountains & Adjacent Plains.

——— 1918—Rosaceae. North Amer. Flora. 22:510-532.

ST. JOHN, H. 1937—Flora of Southeastern Washington and Adjacent Idaho. Students' Book Corporation, Pullman, Washington. 205-210.

WATSON, SERENO 1885—Contributions to American Botany. Proc. Amer. Acad. Arts and Sci. 20:324-350.

The Opuntiae of the Big Bend Region of Texas

Margery Anthony

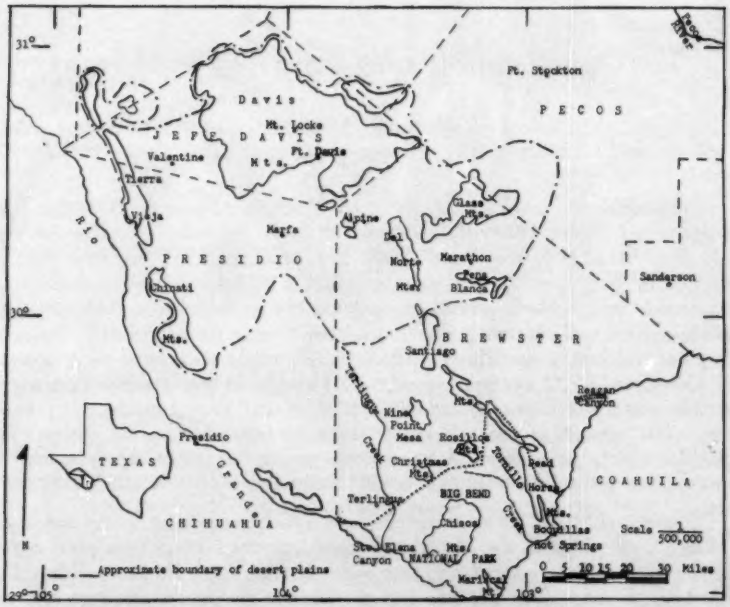
Chico State College, Chico, California

More than 900 members of the genus *Opuntia* (Tournefort) Miller had been named before 1919 when Britton & Rose, by reducing many of the names to synonymy, recognized about 250 valid species. This reduction in number of recognized species was the result of withdrawing some entities to previously unrecognized genera, recognizing the capacity for great variation within species, and redefining descriptions based upon sterile material. Because they are less highly specialized in their modifications than most other genera of Cactaceae the Opuntiae respond more readily to the sharply fluctuating environmental conditions of xerophytic habitats and thus produce many variants. The group has been neglected in field studies because of the painful glochids which make these plants difficult to handle; many otherwise useful and representative collections of desert plants lack *Opuntia* almost entirely.

Opuntiae are the most numerous and most conspicuous components of the rich cactus flora of the Big Bend Region, an area formed by a great curve of the Rio Grande several hundred miles southeast of El Paso (Map 1). Marked physiographic diversity has produced a variety of habitats with a corresponding development of many different populations of *Opuntia*. It is my purpose, by analysis of these natural populations, to 1) determine the significance of vegetative features with respect to the taxonomy of the group, 2) construct a key for identification of each entity, and 3) discuss the significant features of the species. Each entity is fully described in the thesis (Anthony, 1949). Ecological relationships of these cacti are discussed elsewhere (Anthony, 1954).

A total of thirty-one species, hybrids and varieties of *Opuntia* in the Big Bend Region is recognized in this paper. Field observations and collections were made from February to June in 1947, and from March to October in 1948. The dried collection is in the Herbarium of the University of Michigan. Duplicate specimens were grown at the Botanical Gardens of the University of Michigan from 1947 to 1949 in order to test the constancy and value in classification of vegetative characteristics under uniform conditions of heat, humidity and moisture.

ACKNOWLEDGMENTS.—The author expresses sincere appreciation to Professor Harley H. Bartlett, Director of the Botanical Gardens, and to Dr. Elzada U. Clover, Department of Botany, of the University of Michigan, for their encouragement and assistance during this study, which is in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Michigan. Field work was made possible by a Research Assistantship at the Botanical Gardens. Thanks are also extended to Dr. Barton H. Warnock, Chairman, Department of Biology, Sul Ross State Teachers College, Alpine, Texas, and to officials of the Big Bend National Park, for their help. For hospitality, and cooperation in sending material, grateful acknowledgment is made to directors and staff of herbaria of the following institutions: Allan Hancock Foundation at the University of Southern California, University of Arizona, Stanford University, Univer-



Map 1.—Big Bend region and surrounding area.

sity of Michigan, Missouri Botanical Garden, New York Botanical Garden, University of Texas and Smithsonian Institution. Collection data for specimens from these herbaria are cited in the thesis.

HISTORICAL CONSIDERATIONS

The most important early scientific exploration of Trans-Pecos Texas was conducted by the United States and Mexican Boundary Commission Survey (Engelmann, 1859) in 1851-53. Extensive notes and collections were made by C. C. Parry, C. Wright, J. M. Bigelow, G. Thurber, and A. Schott, who sent much valuable living, as well as dried, material to George Engelmann for subsequent identification and publication. Opuntiae of the Big Bend have also been collected by V. Bailey, W. L. Bray, B. Mackensen, C. R. Orcutt, H. C. Cutler, L. C. Hinckley, and B. H. Warnock. Specimens from neighboring Chihuahua have been collected by E. A. Mearns, E. Palmer, J. N. Rose, and E. Stearns.

Engelmann (1849, 1856, 1859) was the first to describe many of the Big Bend cacti but his information was necessarily limited to the often incomplete collections of the earliest botanical explorers. Opuntiae from the Big Bend Region were little represented in the work of D. Griffiths (1908) who, by drawing fine distinctions, described a number of new species; many of these are now reduced in the literature to synonyms or are maintained only as varieties. Most of the Texas species are discussed in the monumental work of Britton & Rose (1919). Their descriptions are brief, with inconsistent choice of charac-

teristics, too narrow ranges of measurement, and obsolete distributional data. "Texas Cacti" by Schultz and Runyon (1930) is largely adapted from Britton & Rose. Some information on the range of various species was obtained from Benson (1940), Boissevain and Davidson (1940), and Tidestrom and Kittell (1941). Bravo (1937) and Ochoterena (1922) have contributed valuable data on the Mexican cacti, many of which occur also in the United States.

Sperry and Warnock (1941) have compiled the most authoritative listing of plant species, including many of the cacti, in Brewster County. A useful key to the plants of the Big Bend National Park (McDougall and Sperry, 1951) has little discussion of the Cactaceae and no key to them.

BRIEF DESCRIPTION OF THE REGION

The study area encompasses Jeff Davis, Presidio and Brewster counties, although the latter, in which are found the Big Bend National Park and greatest topographic diversity, received the most detailed consideration. Physiographically the Big Bend Region includes igneous and sedimentary rocks; shallow to deep and clayey to sandy soils; xerophytic to mesophytic environments; flood plain, desert, arid grassland, encinal and montane habitats occupied by at least thirty-five distinct plant associations (Denyes, 1951). It is a meeting ground for faunal and floral forms of four adjacent biotic provinces.

High desert mountains and mesas, with abrupt increases in altitude, cause sharp changes in vegetative types and associated cacti, as well as producing well-defined races and disjunct distributions through isolation effect (Map I).

CHARACTERISTICS OF TAXONOMIC VALUE

The following features of Opuntiae show enough constancy to be of taxonomic value, despite considerable modification under adverse climatic and edaphic conditions: habit of growth (prostrate, ascending, or arborescent); roots (tuberous or fibrous); joints (cylindrical or flat); distance between areoles on joints; form and color of spines; shape of style; fruits (dry or fleshy, naked or spiny); umbilicus (v-shaped or saucer-shaped); size of seed, and nature of the aril (beaked or beakless, wide or narrow). Skeletons of Cylindropuntia joints show characteristic shapes of gaps in the dictyostele, ranging from long and narrow in *O. davisii* to short, ovate gaps in *O. kleiniae*. Number of spines per areole varies considerably among individuals but some species are characteristically more spiney than others. Bristles, which are intermediate in size between spines and glochids and are borne deflexed from the base of the areole, are typically present in some of the species, typically absent in others.

CHARACTERISTICS SUBJECT TO VARIATION WITHIN SPECIES

Within species greatest variation is expressed in: size of joints and leaves; proportion of spiniferous to naked areoles on joint; number of spines per areole; and length of individual spines. A smaller range of variations occurs in: presence or absence of trunk; amount of glaucous covering of joints; and size and shape of ovary and fruit. These variations may be caused by local differences in water supply, altitude, soil or exposure to sun. Plants growing

in dense shade are often so modified, bearing elongate joints and areoles further apart with fewer spines than is typical, that they can only be identified after experience in growing them under uniform conditions.

Seeds of *O. tortispina* and *O. tunicata* occasionally have double embryos so that two seedlings grow up side by side. One is always larger, greener and more apt to survive. Even if the larger one is early removed at ground level, the weaker pinkish seedling does not succeed. A very low percentage of tricotyledonous seedlings was observed among seeds germinated at the Botanical Gardens. The two cotyledons of a seedling are usually unequal; depending upon the species the cotyledons are long and thin, or short and thick, and with obtuse or acute tips. However, these differences are not great enough to constitute specific characteristics.

Stomata on joints are difficult to observe because of numerous calcium oxylate crystals in the hypodermis. Stomata from cotyledons and leaves of various species show no significant differences in spacing. Length of stomata ranges from an average of 20.9 μ in *O. imbricata* to 43.2 μ in *O. tenuispina*. The rest of the species fall into a graded series between these two averages. Most of the Cylindropuntiae of the study area have somewhat smaller stomata than the Platyopuntiae.

Some of the Opuntiae in the Big Bend Region seem inherently more variable than others. Among the Cylindropuntiae only populations of *O. grahamii* x *schottii* show variability, as would be expected in any hybrid individuals since they tend to resemble one or the other parent. Even the two varieties, *O. leptocaulis* var. *brevispina* and *O. imbricata* var. *argentea*, are very distinct from the typical forms. Among Platyopuntiae greatest variation is evident in populations of *O. engelmannii*, *O. lindheimeri*, *O. phaeacantha* and *O. tortispina* as is reflected in their lengthy synonymy. The fact that the morphological plasticity of these species produces many local races adapted to diverse habitats may explain their wider distribution through the Big Bend Region, with the exception of *O. lindheimeri* which here reaches the western edge of its range.

The following hybrids were found in the area: *O. grahamii* x *schottii*, *O. kleiniae* x *leptocaulis*, and *O. engelmannii* x *phaeacantha*. The latter hybrid of Platoyopuntiae is the only one that forms fertile fruits but the two hybrid Cylindropuntiae reproduce prolifically by fragmentation. Parental species of each hybrid overlap in their flowering periods, are present in the same locality with the hybrids, and the hybrids show intermediate characteristics.

Evolutionary implications of variation within species and of hybridization were discussed in an article on the ecology of these cacti.

KEY TO THE OPUNTIAE OF THE BIG BEND REGION

Since many species of *Opuntia* bloom sporadically the majority of plants have only vegetative characteristics as a clue to identity. Furthermore, reproductive organs of closely related species, such as in the *O. engelmannii*—*O. phaeacantha* complex and the *O. grahamii*—*O. schottii* complex, are variable enough that clear-cut distinctions based upon these alone would be difficult to observe in the field without long experience. Herbarium specimens of flowers and fruits are also difficult to distinguish because of the great distor-

tion of the succulent tissue in drying. For these reasons the key stresses habit and other vegetative features which are more readily recognized in the field.

Species are numbered to follow the sequence of relationship used by Britton & Rose (1919). Discussion of each entity emphasizes points not covered by those authors. Complete descriptions of new forms are included here to facilitate future reference but their original publication occurred with the microfilming of the thesis in 1951.

1a. Joints cylindrical ..... CYLINDROPUNTIA 2a

1b. Joints flattened to form "pads" ..... PLATYOPUNTIA 12a

2a. Branches ascending, joints linear-oblong, spines sheathed 3a

2b. Branches prostrate, only terminal joints ascending, joints clavate, tubercles broad, spines scabrous, without sheaths except when very young 10a

3a. Plant a low clump, shrub or tree, joints mostly more than 16 mm in diameter, tubercles strong, laterally compressed 4a

3b. Plant a twiggy shrub, ultimate joints less than 16 mm in diameter, readily detached, of two distinct kinds; some long, others always short and relatively spineless, tubercles weak or absent 7a

4a. Shrubs or trees with definite, erect trunk 5a

4b. Low clump to 5 dm high with many short erect branches, ultimate joints mostly 2.5 cm in diameter (dwarf forms noticeably smaller), tubercles about 30 mm long, 3 mm wide, 12 mm high, spines yellow with whitish sheaths, flower yellow. (figs. 8 & 9) ..... 8. *O. tunicata*

5a. Tall shrubs to trees, ultimate joints 1.5-4 cm in diameter, flower magenta 6a

5b. Small shrubs, up to 7.5 dm high, ultimate joints .6-2 cm in diameter, typically wrinkled, tubercles about 25 mm long, 7 mm wide, 7 mm high, spines yellow or rufous, with yellow sheaths, flower yellow. (fig. 3) ..... 5. *O. davisii*

6a. To 45 dm in height, tubercles 30 mm long and 8 mm high or more, central spines yellow or reddish brown, with dull white sheaths. (fig. 6) ..... 6. *O. imbricata*

6b. To 12 dm in height, tubercles only 20 mm long and 5 mm high, spines silver with silver sheaths. (fig. 7) ..... *O. imbricata var. argentea*

7a. Ultimate joints 6-15 mm in diameter, short ones mostly 5-7 cm long, arising at acute angles and curving gradually upwards, surface somewhat tuberculate, flower rose or pinkish, 2.5-4 cm long 8a

7b. Ultimate joints 5-6 mm in diameter, short ones mostly 2-4 cm long, arising mostly at right angles and curving sharply upwards, surface not tuberculate, flower lemon yellow, about 2.2 cm long 9a

8a. Ultimate joints usually more than 8 mm in diameter, short joints mostly 7 cm long, flower dull rose, about 4 cm long. (fig. 2) ..... 3. *O. kleiniae*

8b. Ultimate joints usually less than 8 mm in diameter, short joints mostly 5 cm long, flower pinkish brown, 2.5-3 cm long. (figs. 1 & 4) 4. *O. kleiniae x leptocaulis*

9a. Spines 3-5 cm long, with conspicuous persistent sheaths ..... 1. *O. leptocaulis*

9b. Spines .8-2.8 cm long, with fugacious sheaths. (fig. 1) ..... 2. *O. leptocaulis var. brevispina*

10a. Spines acicular, mostly terete, only a few flattened, leaves longsubulate, joints 4.5-7 cm long, tubercles weak. (fig. 12) ..... 10. *O. grahamii*

10b. Spines subulate, mostly flattened, leaves short subulate 11a

11a. Joints 2.5-9 cm long, strongly tuberculate, spines 1.5-2 mm wide. (fig. 12) ..... 9. *O. schottii*

11b. Joints 2.5-6.3 cm long, tubercles only moderately developed, spines .5-1.3 mm wide (fig. 13) ..... 11. *O. grahamii x schottii*

12a. Plant a large bush, usually more than 3 dm high and 10 dm wide, surface of

joints glabrous or pubescent 13a

12b. Plant a small bush, usually less than 3 dm high and 10 dm wide, surface of joints glabrous 31a

13a. Surface of joints glabrous, spines typically present 14a

13b. Surface of joints pubescent, spines never present, branches mostly ascending, joints relatively thick 30a

14a. Mature spines predominantly orange, yellow or white 15a

14b. Mature spines predominantly red to brown or darker colors 22a

15a. Mature spines predominantly white 16a

15b. Mature spines predominantly yellow or shades of orange 18a

16a. Young joints not wrinkled, longer spines flattened, only slightly twisted, young spines mostly white or black with dark bases 17a

16b. Young joints often wrinkled, longer spines terete, much twisted, young spines burnt yellow (fig. 11) ..... 14. *O. tortispina*

17a. Branches mostly ascending, joints short-obovate to orbicular, young spines white with dark bases, mature spines 3-5.6 cm long, fruit large, pyriform ..... 24. *O. engelmannii*

17b. Branches spreading, slightly ascending, joints long-obovate with attenuate bases, young spines black, mature spines 5.5-7.3 cm long (fig. 28) ..... 25. *O. engelmannii var. wootonii*

18a. Branches all ascending, to 25 dm in height, joints with elongate cow-tongue shape, spines acicular, bristles absent, flower yellow (fig. 5) ..... 27. *O. linguiformis*

18b. Branches spreading or gradually ascending, joints obovate to orbicular, spines subulate 19a

19a. Spines elliptic to flat in cross-section, only slightly twisted 20a

19b. Spines terete, much twisted (fig. 11) ..... 14. *O. tortispina*

20a. Marked contrast between young white spines, mature yellow spines and old black spines, bristles often present. (fig. 18) ..... 21. *O. azurea*

20b. No marked contrast, young spines mostly yellow, mature spines yellow to orange-red, old spines becoming gray to black, bristles absent 21a

21a. Areoles circular, elevated and conspicuous, spines little curved, fruit large, pyriform, to 7 cm long (fig. 29) ..... 28. *O. lindheimeri*

21b. Areoles long-elliptic, not conspicuous, spines mostly curved downward, fruit globular, to 4.5 cm long (figs. 26 & 29) ..... 29. *O. lindheimeri var. chisosensis*

22a. Spines subulate 23a

22b. Spines acicular, mostly from upper or marginal areoles 27a

23a. Branches ascending abruptly to form a tall bush, joints somewhat tuberculate, 2-4 rufous spines and 2 conspicuous bristles in an areole, ovary and fruit spiny (figs. 22, 23 & 24). ..... 23. *O. spinosibacca*

23b. Branches spreading or ascending gradually, joints not tuberculate 24a

24a. Areoles distant, fruit naked 25a

24b. Areoles closely-set, fruit spiny, joints mostly orbicular, spines dark reddish brown with yellow tips (fig. 16) ..... 15. *O. strigil*

25a. Areoles elevated, spines somewhat flattened, not annulately marked 26a

25b. Areoles not elevated, spines mostly terete, often annulately marked, young spines rufous and white, flower usually less than 6.5 cm long, seeds to 7 mm in diameter (fig. 25) ..... 22. *O. phaeacantha*

26a. Young spines white, mature spines white to reddish brown, fruit large, pyriform, to 6.5 cm long ..... 24. *O. engelmannii*

26b. Young and mature spines reddish brown to black, fruit variable (fig. 27) ..... 26. *O. engelmannii x phaeacantha*

27a. Branches spreading and ascending, joints mostly orbicular or short-obovate 28a

27b. Branches mostly spreading, joints obovate 29a

28a. Joints 6-12 mm thick, spines 1-10 per areole, some flattened, mostly spreading downwards, not annulately marked. (fig. 19) ..... 17. *O. setispina*

28b. Joints mostly less than 6 mm thick, spines mostly 2-3 per areole, terete, spreading upwards, annulately marked. ..... 19. *O. macrocentra*

29a. Branches spreading, a few ascending vertically, joints less than 15 cm long, areoles less than 20 mm apart (fig. 21) ..... 20. *O. macrocentra var. minor*

29b. Branches spreading, joints more than 15 cm long, areoles more than 25 mm apart (fig. 20) ..... 18. *O. tenuispina*

30a. Areoles mostly about 16 mm apart, joints long obovate, outer perianth segments broad-lanceolate and not swirled (fig. 14) ..... 12. *O. rufida*

30b. Areoles mostly about 12 mm apart, joints short obovate to short elliptic, outer perianth segments narrow lanceolate and swirled (fig. 15). ..... 13. *O. rufida var. tortiflora*

31a. Branches creeping, only terminal joints ascending, roots fibrous, joints obovate to elliptic, areoles closely-set, spines acicular, from all but lowermost areoles, fruit spiny and dry 32a

31b. Plant inconspicuous; branches, with only 2-3 joints, ascending, to 2.5 dm in height; roots tuberous, with milky juice; flower rose-red; fruit naked, pale purple (fig. 17) ..... 16. *O. pottsii*

32a. Joints obovate with somewhat tuberculate surface, hairs absent (fig. 32)..... 31. *O. polyacantha*

32b. Joints long-elliptic, not tuberculate, long hairs conspicuous in lowermost areoles of older joints (fig. 31) ..... 30. *O. trichophora*

1 OPUNTIA LEPTOCAULIS DC. Mém. Mus. Hist. Nat. Paris 17:118. 1828.

Distribution: GENERAL.—Arizona, New Mexico, Texas, southern Oklahoma and the northern states of Mexico (Chihuahua, Coahuila, Hidalgo, San Luis Potosi, Sonora and Tamaulipas). LOCAL.—Grassland and desert associations of Brewster, Presidio and Jeff Davis counties, at altitudes from 1900 to 5000 feet.

This species is aptly named for its pencil-thin joints. Of wide-spread occurrence throughout the Big Bend Region the plants vary in form from low bushes with numerous primary stems to erect, almost arborescent bushes producing only one or two primary stems which in turn give rise to secondary branches about 8 cm above the ground.

The majority of the readily-detached ultimate joints are spineless and about 3 cm long. The remainder are more variable in length (from 3 to 9.5 cm long). In contrast to *O. kleiniae*, *O. leptocaulis* has more of the very short joints which usually arise at right angles. These, and the longer joints, curve up sharply, unlike the gradually upward-curving ultimate joints of *O. kleiniae*. There are rarely more than two joints at a node. Stems of this species are yellow-green in color with purple blotches below the areoles; those of *O. kleiniae* are gray-green with a purple tinge around the areoles or over the entire ventral surface. Diseased joints of *O. leptocaulis* proliferate prodigiously, producing a "witches' broom" effect.

Flowers arise along the terminal halves of longer joints, are inconspicuous, and in contrast to those of other Opuntiae, do not open until late afternoon, closing late at night. The blooming period extends from the middle of June to as late as September. Fruits often remain on the plant a year or longer, are spineless, and capable of proliferation. Each fruit bears a few seeds which have a narrow beakless aril. The vascular gaps in the skeletal

lattice are relatively small, mostly short and oval with much thick wood between.

Many varieties have been described, but the only evident variant in the Big Bend Region is var. *brevispina*. The species is reported by Britton & Rose (1919) to hybridize with *O. imbricata*. I found no such hybrids, although the two species occur together frequently and their flowering periods overlap. A hybrid between *O. leptocaulis* and *O. kleiniae* was collected and is described below.

2 OPUNTIA LEPTOCAULIS var. BREVISPINA Engelmann in Proc. Amer. Acad. 3:309. 1856

This short-spined variety of the well-defined species occurs commonly throughout the southwest and has long been recognized by taxonomists. It is characterized by shorter spines (6-28 mm long) which lack sheaths or have closely-fitting fugacious sheaths and fewer of the long ultimate joints (fig. 1). Spines often spread downward instead of at right angles as in the typical form. It sometimes occurs with the typical *O. leptocaulis* which negates the possibility of its being only an edaphic form.

3 OPUNTIA KLEINIAE DC. Mém. Mus. Hist. Nat. Paris 17:118. 1828

Distribution: GENERAL.—Southern New Mexico, western Texas, Coahuila, Sonora and states in central Mexico. LOCAL.—Infrequent along creek bottomlands in the Davis Mountains and in arroyos on desert flats, also along the Rio Grande from Presidio to Pecos River, at altitudes from 1900 to 4800 feet.

The specific epithet emphasizes the resemblance to members of the genus *Kleinia*, a succulent composite endemic to Africa.

These large profusely-branched bushes are difficult to discern at a distance, since they are usually growing with other tall shrubs. Three or more main branches arise from the base of the plant, whereas *O. leptocaulis* typically has only one or two main trunks (fig. 2). There are two types of ultimate joints in *O. kleiniae* as is also characteristic of *O. leptocaulis* and *O. leptocaulis* x *kleiniae*. The majority of the joints are short (in *O. kleiniae* about 7 cm long, and spineless); the others are highly variable in length (in *O. Kleiniae* from 8 to 25 cm long). Both types of ultimate joints in *O. kleiniae* arise at angles somewhat less than 90° to the main branch and curve gradually upward. As many as four verticillate branches may arise at a node. Joints are readily detached and spines are strongly barbed. There are usually 2-9 spines in an areole.

The flowering period lasts from late May to late August, with dull rose flowers borne in profusion. Mature fruits develop within two months. Under adverse conditions, or if detached while still green, these fruits readily proliferate, producing shoots and roots, and may serve for vegetative reproduction. Seeds are relatively large (to 5 mm in diameter) with a narrow and beaked aril. Seedlings are frequently found in thickets of these bushes. The skeletal pattern is characterized by oval gaps which are relatively short and wide.

4 **Opuntia kleiniae x leptocaulis hybr. nov.**

Erecta, usque ad 15 dm alta; articulis plerisque 5 cm longis, 8 mm diametro, paulum tuberculatis; areolis elevatis 2 mm; spina 1, paululum deflexa, spinis setosis absen-

tibus; floribus 3.2 cm longis, 1.5 cm latis, magnitudine intermediis inter parentes, interioribus segmentibus fusci-rubellis; fructibus 1.4-1.8 cm longis, 1 cm latis; seminibus 4 mm diametro. Specimen typicum secus rivulum dictum "Musquiz Creek," prope montem "Mitre Peak," Jeff Davis Co., Texas, siccatum conservatum est sub numero 513 in Herb. Univ. Mich. et vivum sub numero 19215 in Hort. Mich.

Plant a densely-branched bush to 15 dm high with crown about 20 dm across; trunk to 5 cm in diameter; branches ascending; roots fibrous; joints intermediate between parents in size, ascending at acute angles, more like *O. Kleiniae* in appearance, short joints mostly 5-7 cm long, to 8 mm in diameter, slightly tuberculate with protuberances to 2 mm high, glaucous, gray green; leaves subulate, short mucronate, 3-7 mm long, 1.5 mm wide, green; areoles distant, about 12 mm apart, bearing glands, obovate, to 4.5 mm long and 3 mm wide, becoming larger and elevated in age; wool abundant, yellow or tan; spines 1 per areole, from uppermost areoles, stout, at right angles to stem or directed slightly downward, short joints spineless, young and mature spines white or purplish-brown with yellow tips, sheath white with long orange-tip, persistent, finally becoming gray and shaggy in age; bristles 2-4, caducous; glochids inconspicuous in small dense tufts in upper end of areoles, bright orange with yellow bases, to 15 mm long in older areoles; flower intermediate between parents in size, about 3.2 cm long, and 1.5 cm across with perianth segments in 4 whorls, outer segments short-oblong, mucronate, not recurved, inner segments pale pinkish brown with darker trace, broadly spatulate, mucronate, to 1.3 cm long and 8 mm wide; filaments greenish white below, pink above, 5 mm long, anthers yellow; style white below, pink above, bulbous above base, long and thin, to 12 mm in length, stigma lobes 4, creamy yellow, 2.5 mm long; ovary long conic with tapering base, to 2 cm long and 1 cm in diameter, with distant areoles bearing minute, subulate leaves, tawny wool, dense tufts of reddish-orange glochids; lacking bristles and spines; fruit small, drying to orange, narrowly obconic, with attenuate base, mostly sterile, to 1.8 cm long and 1 cm in diameter when mature, with minute areoles, short reddish-orange glochids, spines lacking; umbilicus v-shaped, 5 mm deep; seeds yellow, beakless, faintly notched at hilum, large, 4 mm in diameter, to 2 mm thick, aril 0.5 mm wide.

Type locality: With Acacia and Prosopis in thickets along bottomland of Musquiz Creek, south of Davis Mountains and east of Rt. 118, Jeff Davis County, Texas, at 4400 ft. altitude.

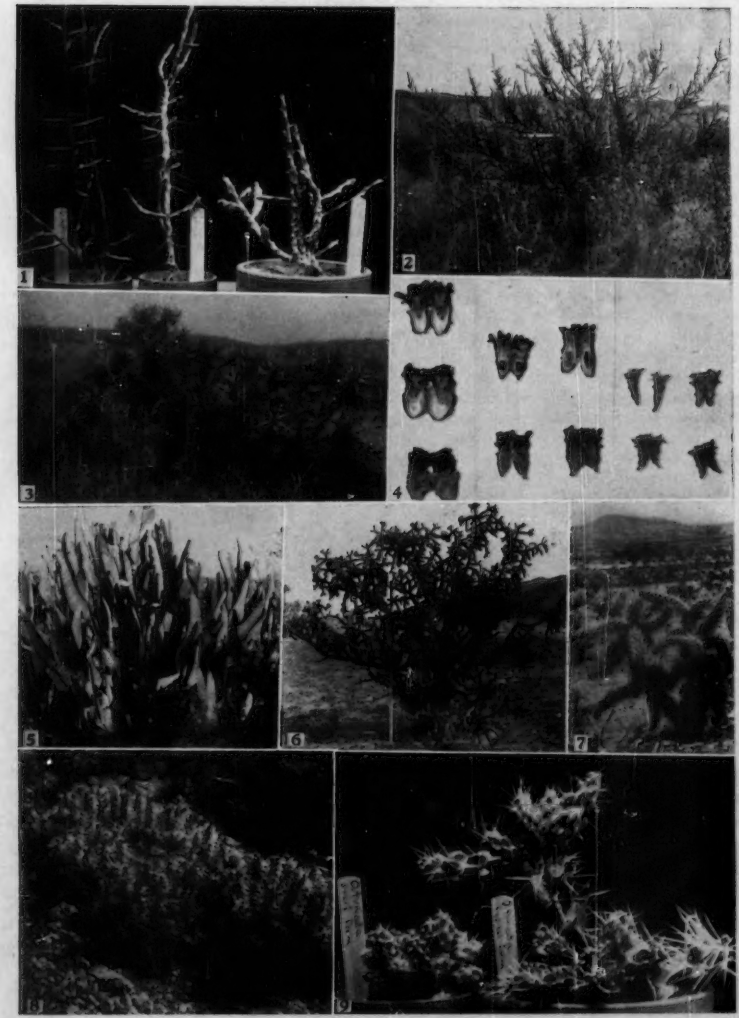
Distribution: Found only at type locality.

In most respects these hybrid plants resemble *Opuntia kleiniae* more closely than *O. leptocaulis* (figs. 1 and 4) but size of the entire plant is somewhat smaller; the short joints characteristically curve up more sharply; tubercles are less evident and bear smaller areoles; areoles usually have only one long spine, pointing downward; mature plants lack bristles; and seedlings have more slender cotyledons.

Flowering coincides with that of the parents, both of which bloom from June to August. Young fruits were collected in late September.

Both parents were locally abundant at the locale of this hybrid. The smaller stature of the hybrid may arise from some disparity in chromosome numbers of the parents. The peculiar color of the flowers may conceivably be interpreted as a purely visual effect of the inheritance of yellow pigment in certain cells (probably sub-epidermal) from one parent and purple (probably in epidermal cells) from the other parent, the combined effect being brownish.

Collections.—JEFF DAVIS CO.: (Type specimen) infrequent with Acacia and Prosopis in thickets along bottomland of Musquiz Creek, east of Mitre Peak, along Rt. 118, 4400 ft., June 4, 1948, No. 513; Aug. 24, 1948, No. 1044; Sept. 22, 1948, No. 1377 (a and b).



Figs. 1-9.—1. l. to r.) *O. leptocaulis* var. *brevispina, O. kleiniae x leptocaulis* and *O. kleiniae.* All have produced some new growth under cultivation; 2. *O. kleiniae* with fruits, in catclaw thicket with short grass along Musquiz Creek; 3. *O. davisii* in fruit, with grassland vegetation south of Marathon; 4. Flowers of the hybrid (center) are intermediate in size and color between those of *O. kleiniae* (left) and *O. leptocaulis* (right); 5. *O. linguiformis* in abandoned Mexican garden along Tornillo Creek, Big Bend National Park; 6. *O. imbricata* in bloom, with short grass association east of Alpine; 7. Young plant of *O. imbricata* var. *argentea;* north end of Mariscal Mountain; 8. *O. tunicata* with flowers and immature fruits; 9. Dwarf form of *O. tunicata* (left) with joints about 1/3 the size of those of the typical form (right).

5 OPUNTIA DAVISII Engelmann and Bigelow, Pac. R.R. Rep. 4:49. 1856

Distribution: GENERAL.—Western Texas, eastern New Mexico, southwestern Colorado, and southwestern Oklahoma. LOCAL.—Grassland plains of northern Presido and Brewster counties, at altitudes of 4400-5000 feet.

Engelmann and Bigelow (1856) named this *Opuntia* in honor of Jefferson Davis, the Secretary of War under whom the scientifically valuable Pacific railway surveys were made.

The erect shrub stands out at some distance with its straw-colored, loosely-sheathed spines completely obscuring the stems (fig. 3). The untidy appearance of the plants is due to the great abundance of spines from closely set areoles. The trunk is woody and densely-branched with several verticillate, easily-detached joints at each node. Spines are of two sorts, 5-7 are longer, subulate, reddish brown with persistent sheaths; 2-4 radially deflexed from the outer margin of the areole are shorter, acicular, all yellow or straw-colored, and without sheaths. Hester (1939) described a plant from this region otherwise resembling *Opuntia davisii* but with tuberous roots.

The flowering period is short, a few weeks in late June and early July. One to three seeds may be found in a fruit although many of the fruits are sterile. The seeds are about 3.5 mm in diameter with a thin beaked aril. The large vascular gaps on old stems are long, narrow and actuely-pointed.

Individuals occur singly or as many as ten may be scattered locally. In the Big Bend Region the species is restricted to arid grassland associations, particularly in broad wash areas.

6 OPUNTIA IMBRICATA (Haworth) DC. Prodr. Sys. Nat. Reg. Veg. 3:471.1828

Distribution: GENERAL.—Central to southeastern Colorado, Oklahoma, Texas, New Mexico, Arizona, and the high plains of Mexico. Reported from Utah (Rydberg, 1917) and from Kansas. LOCAL.—Woodland, grassland and desert associations in Brewster, Presidio, and Jeff Davis counties, at altitudes from 2700 to 6200 feet.

The specific epithet refers to the sublobular tubercles which overlap on the stem. The sturdy trunk reaches a height of one or more dm before it divides into at least three primary branches. At each node two to six verticillate secondary branches arise, usually at right angles and curving upwards. One of these generally continues growth to form new nodes (fig. 6). Each areole bears 6-14 reddish-brown, central spines and 3-10 shorter, gray, radial spines.

Along washes and other runoff areas plants may be relatively spineless or bearing very short spines and the joints are often more turgid with broader tubercles. The surface is lighter green with a less glaucous covering.

Flowering is prolific over a period from the end of April to as late as the end of July with the peak in May; two to six flowers are borne in a cluster near the tips of ultimate joints. Fruits ripen within two to three months but are long-persistent on the plant so that two years' crop may be present at once. Occasionally these fruits undergo vegetative reversion and develop into joints with the locule imbedded in the upper part. Seeds are smooth, with a narrow slightly beaked aril. Seedlings are surprisingly abundant considering how seldom one sees seedlings of other cactus species. Undoubtedly

their prolific production allows greater chance for some surviving. Skeletons of branches are distinguished by a pattern of long and wide vascular gaps.

7 Opuntia imbricata var. argentea var. nov.

Similis formae typicae sed articulus crassioribus quam in forma typica; spinis vaginisque argenteis. Specimen typicum ex monte dicto "Mariscal Mountain, Big Bend National Park, Texas" siccatum conservatum est sub numero 280 in Herb. Univ. Mich. et vivum conservatum est sub numero 18830 in Hort. Mich.

Plant a small, erect shrub, to 12 dm high, with crown to about 10 dm. across; trunk up to 7.5 cm in diameter; branches many, spreading to erect; roots fibrous; joints relatively large, to 20 cm long, 1.5-4 cm in diameter; tubercles 2 cm long, 5-12 mm wide and 5 mm high, heavily glaucous, silvery green; leaves long-subulate, apiculate, 10-17 mm long, 1.5 mm wide; areoles closely set, to 20 mm apart, long-oval, 5-7 mm long, 3-4 mm wide; wool abundant, pale yellow, gray in age; spines 11-21, from all except lowermost areoles, subulate, elliptic in cross-section, young spines white or pink with greenish base, older spines silvery with pinkish bases and silvery white sheaths, finally becoming gray, 6-14 central spines longer, to 2 cm long, spreading, 5-7 radial spines shorter, to 1.8 cm long, spreading deflexed; bristles indistinguishable; glochids inconspicuous in compact row along upper margin of areole, white with green bases when young, pale yellow in older areoles; scarcely 1 mm long; flower about 5 cm long, and to 5 cm across, with perianth segments in 4 whorls, outer segments pink with olive trace, apiculate, oblong, inner segments reddish-purple, broadly spatulate, apiculate, to 2.5 cm long and 1.4 cm wide; filaments magenta, 9 mm long; style bulbous just above base, to 18 mm long, stigma lobes 7-9, 5 mm long; ovary short conic, truncate, about 1.5 cm long, and 1.5 cm wide, with large, closely set areoles, uppermost ones bearing small subulate leaves, abundant tawny wool, few minute white glochids and 1-2 long white bristles; fruits and seeds unknown.

Type locality: Mariscal Mountain, Big Bend National Park, Brewster County, Texas.

Distribution: Around Mariscal Mountain only, observed on northern and eastern slopes, eastern pediment, and west of Solis Ranch in Prosopis thickets of Rio Grande Plain, Big Bend National Park, at altitudes from 2000 to 2400 feet.

This variety differs from the typical *O. imbricata* in its lower stature, smaller tubercles so that the areoles are closer together, and spines which are silvery throughout, hence the varietal epithet. Appearance in the field is chubby in comparison with the typical form (fig. 7). Flowers open early in April. Mature fruits were not obtained.

A specimen, transplanted from the type locality at 2300 feet to Victor Pierce Ranch in the Glass Mountains at 4300 feet, survived the unusually cold winter (minimum temperature of 0°F) of 1947-48, and was growing vigorously when re-collected. This adaptability augers well for future spreading and establishment beyond the present small range of distribution.

A living specimen at the Botanical Gardens has produced a number of new joints which are more abundant, arise at more acute angles, and are spinier than joints of the typical *O. imbricata* growing in the same greenhouse.

Collections.—BREWSTER CO.: Locally abund. with Larrea-Agave, 2000 feet, on pediment 4 mi. east of Mariscal Mt., Big Bend National Park, April 7, 1947, No. 23; rare, with Prosopis on sandy wash along Rio Grande near Solis Ranch house, Big Bend Nat. Park, April 28, 1948, No. 276; (type specimen) abundant with *Agave lechuguilla*, 2500 ft., on northern slope of Mariscal Mt., Big Bend Nat. Park, Apr. 29, 1948, No. 280; with Bouteloua-Juniperus association in transplant plot on Victor Pierce Ranch in Glass Mts., limestone soil, 4300 ft., (Orig. from pediment e. of Mariscal Mt., Apr. 7, 1947), Sept. 12, 1948, No. 1163.

8 OPUNTIA TUNICATA (Lehman) Link and Otto, in Pfeiffer Enum. Cact. 170. 1837

Distribution: GENERAL.—Oriente, Cuba; Mesa Central and Highlands of central Mexico; Ecuador; Peru; Chile; locally in Glass Mountains, Big Bend Region of Texas. LOCAL.—In an area of about one-half square mile on the southeastern slope of an outlier of the Glass Mountains, in southwestern Pecos County, Texas. First known scientific observation of this locality was by Dr. B. H. Warnock, Department of Biology, Sul Ross State Teachers College, who very kindly brought it to my attention.

The specific epithet from "tunicatus" L. refers to the sheaths which clothe the spines. The sheen of these papery-white sheaths, which almost obscure the stem in their abundance, strikes the eye with patches of reflected light, even at some distance. The plants grow in low-spreading clumps to 3.5 dm high and 7.1 dm across, with an accumulated debris of dead branches among the green ones. Myriads of ants are attracted by glandular secretions from the living areoles.

A thick, woody, half-buried stem, which may attain a length of 30 cm, creeps along the ground sending up branches. Clumps are composed of about 50-60 main stems which are erect, to 20 cm in height and 5 cm in width, and bear ultimate joints to 9 cm long and 2.5 cm in diameter (fig. 8). Joints are very readily detached and root wherever they fall. The whitish yellow spines are of several lengths; one up to 5.2 cm long, 2-4 shorter, and 1-2 much shorter, only reaching 3 cm in length. Two thin bristles reaching 8 mm in length are freqeuntly found accompanying spines and glochids in the areoles.

As many as seven flowers may be borne in a cluster toward the tips of ultimate joints. The perianth segments are loosely arranged in three whorls. In 1948, the flowering period extended from about June 24 to early July, and fruits matured in two months. The obconic fruit is often sterile and may proliferate, especially if detached. Seeds when present average 3.2 mm in diameter with a thin aril. Of 15 seeds planted at the Botanical Gardens, only one germinated and it happened to have a double embryo.

A dwarf form, scattered abundantly around the larger, typical plants, is distinguished by its miniature size (mostly 7 cm high) and shorter, more bristle-like spines (fig. 9). The creeping stem is 10 cm long, 1.5 cm wide, and there is a short erect trunk. Joints are short-obovate and clavate, about 3.5 cm long and 1 cm wide. Areoles measure up to 2.5 cm long and contain 1-2 spines, 2.4 cm long or less, and 2-4 bristles, strongly deflexed, to 5 mm long. Neither flowers nor fruits were found on dwarf plants. These dwarf forms develop from detached, proliferating, terminal joints and fruits, and from natural seeding. The larger typical form seems to arise from detached main branches. Further research with living material will be carried out to determine the complete origin of both forms and significance of their relationship.

9 OPUNTIA GRAHAMII Engelmann, Rep. U.S. & Mex. Bound. Surv. II, Pt. 1, p. 55. 1859

Distribution: GENERAL.—Southern New Mexico, western Texas, and adjacent parts of Chihuahua in Mexico. LOCAL.—Desert associations in southern Brewster and Presidio counties, at altitudes from 1900 to 3400 feeet.

As head of the scientific corps of the United States and Mexican Boundary Commission, Colonel James D. Graham was responsible for much of the botanical material sent to Engelmann, who gratefully named this cactus in his honor.

This prostrate, clump-forming species is much more common in the Big Bend Region than the closely related *O. schottii*. Each main branch in the clump usually produces three, linearly arranged, joints; these give rise to secondary branches which are curved and ascending toward the tips. As branches creep along the ground, fibrous roots develop from basal areoles of each joint. Tuberous roots are generally found near the center of the clump where the roots are older and better established. The "tubers" of *O. grahamii* are smaller and less abundant than those of *O. schottii*. The oldest joints are apparently always infected with fungus and tend to disintegrate, or it may be that the older parts of the plant die naturally, and that fungus infection is secondary. In either event many small independent plants become established around a central mass of dead and dying stems. Terminal joints also break off easily to form new individuals. Clumps are often found around the bases of creosote bushes; either fragments blow and lodge there, or they are less disturbed and therefore have a better chance to develop under such conditions. The mounds, with a tangle of creeping branches, are nuclei of deposition for wind-carried debris and soil particles so the oldest joints are usually covered by soil and the mound grows upward as well as outward (fig. 10). There are usually 4-6 spreading, dull red, central spines and 2-6 shorter, deflexed, white, radial spines in each areole on the upper half of the joint. Young spines occasionally have evanescent white sheaths.

Few, but conspicuously large, flowers are formed, usually in March and early April although Engelmann (1859) gives the flowering period as June; it may vary with the rains. Flowers are often as long as the joints themselves. By September, a few mature dry bristly fruits are found, but most of them are sterile. The large seeds (5 mm in diameter) have a narrow beaked aril.

10 OPUNTIA SCHOTTII Engelmann, Rep. U.S. & Mex. Bound. Surv. II, Pt. I., p. 54. 1859

Distribution: GENERAL.—Southern and western Texas, and northern Mexico. LOCAL.—Desert associations in southern Brewster and Presidio counties, at altitudes from 1500 to 3800 feet.

Arthur Schott was another active botanical collector with the United States and Mexican Boundary Survey of 1851-1853 and sent many species of cacti to Engelmann.

In its most typical form, this species is easily distinguished from *O. grahamii* by stronger and broadly-flattened spines, larger and relatively longer joints, and more prominent and elongate tubercles (fig. 12). There are usually 2-5 longer, spreading, grayish-brown, central spines; 1-4 shorter spines below these; and 5-8 short, deflexed, white, radial spines, in areoles on the upper two-thirds of the joint. Mounds are of the same general formation as those of *O. grahamii* but are larger. Joints have a very spiny appearance and readily become attached to passing animals.

Flowers are even rarer than those of *O. grahamii;* the species seems to be

losing its ability to reproduce sexually while becoming highly successful with asexual means of propagation. Flowers, sometimes as long as the joints, may be found from the middle of April to early May. Fruits which mature about a month after flowering, are dry, shrunken, abundantly armed with bristles, and often sterile. Rarely a fruit may metamorphose directly into a joint. Seeds are similar to those of *O. grahamii*.

11 Opuntia grahamii x schottii hybr. nov.

Prostrata; articulis 5-6.3 cm longis, 1.5-2.5 cm latis, grandioribus quam in *O. grahamii*, eis *O. schottii* fere aequalibus; tuberculis magnis, augustioribus quam in *O. grahamii*; spinis 3-9; subcompressis; floribus flavis, segmentis perianthii exterioribus longis, angustis. Specimen typicum ex loco dicto "Hot Springs, Big Bend National Park, Texas" siccatum conservatum est sub numero 856 in Herb. Univ. Mich. et vivum conservatum est sub 19605 in Hort. Mich.

Plant forming low mound about 10 cm high and 6 dm in diameter; trunk absent; branches creeping, ascending at tips; roots mostly fibrous, occasionally with several tubers to 10 cm long and 1 cm wide; joints clavate or short obovate, 5-6.3 cm long, 1.5-2.3 cm wide; tubercles broad, to 8 mm long, 4-5 mm wide, and 5-7 mm high, glaucous, apple green, purplish on tubercles; leaves short-subulate, apiculate, to 7 mm long and 2 mm wide, purplish-green; areoles 10-15 mm apart, circular, large, to 4 mm in diameter; wool abundant, white; spines 1-10, from all but lowermost areoles, scabrous, subulate, flat above, convex below, with bulbous bases, young spines white with pinkish bases and pale yellow tips, older spines purplish-brown with white edges, 3-4 spines longer, to 4.6 cm long, spreading, 1-5 spines shorter, to 1.9 cm in length, spreading, 2-4 radial spines even shorter, to 1.7 cm long, terete, deflexed, white; bristles indistinguishable; glochids conspicuous, pale yellow when young, white to gray and up to 12 mm long and spine-like in older areoles; flower about 7 cm long and 5 cm across with perianth segments in 4-5 whorls, outer segments long lanceolate to narrow conic, green tipped with pink, inner segments bright yellow, spatulate, apiculate, slightly fimbriate, to 2.8 cm long and 1.8 cm wide; filaments red, 8 mm long; style creamy, narrow, to 25 mm long, stigma lobes 5, green, 5 mm long; ovary thin-obconic to 4.5 cm long, and 1.1 cm in diameter, with large areoles, bearing subulate leaves, abundant white wool, numerous white glochids and several white bristles near rim of ovary; immature fruit as in *O. schottii* with areoles bearing abundant white glochids and many long white bristles; umbilicus v-shaped, 10 mm. deep.

Type locality: Sandy upper reaches of Tornillo Creek, northeast of Grapevine Hills, Big Bend National Park, Brewster County, Texas.

Distribution: Desert shrub belt in southern Brewster and Presidio counties, Texas.

Joints of this hybrid are smaller with shorter and finer spines than those of *O. schottii*, but the spines are more flattened and tubercles are stronger than those of *O. grahamii* (fig. 13). Flowers are sparse, a characteristic common to both parents, and appear in April. Distribution of the hybrid forms is approximately the same as that of the parents, throughout southern Brewster and Presidio counties.

Collections: BREWSTER CO.—With Larrea-Agave on limestone ridges, 2 mi. n.e. of Solis Ranch, 1950 ft., Big Bend Nat. Park, Apr. 15, 1947, No. 31b; with Larrea on limestone flat; n. of Hot Springs, 2000 ft., Big Bend Nat. Park, Apr. 18, 1947 No. 37a; in draw n. of Talley Mt., 2600 ft., Big Bend Nat. Park, May 4, 1947, No. 83; (type speecimen) with Larrea, on Tornillo Flats, 2800 ft., Big Bend Nat. Park, July 30, 1948, No. 856; with Larrea, e. of Nine-Pt. Mesa, 3200 ft., Aug. 3, 1948, No. 909; with Larrea, 15 mi. n. of Terlingua, along road to Alpine, Sept. 14, 1948, No. 1181; with Larrea-Fouquieria, flats just n. of Ste. Elena Canyon, 2200 ft., Big Bend Nat. Park, Sept. 15, 1948, No. 1246; with Larrea, just s. of Nine-Pt. Mesa, 3400 ft., Sept. 26, 1948, No. 1267; with Dasylirion-Agave and some Larrea along Dabney-Moody ranch rd. in to Nine-

Pt. Mesa, 3700 ft., Sept. 28, 1948, No. 1283. VAL VERDE CO.—6 mi. w. of Pecos River, Mar. 31, 1948, No. 205.

12 OPUNTIA RUFIDA Engelmann, Rep. U.S. & Mex. Bound. Surv. II, Pt. 1, p. 51, 1859

Distribution: GENERAL.—Texas and northern Mexico. LOCAL.—Desert flats south from approximately latitude 30°, in southern Brewster and Presidio counties, characteristically on steep, rocky walls along the river and in canyons, at altitudes from 1600 to 4100 feet.

The specific epithet refers to conspicuous reddish-brown tufts of glochids on the spineless pads. The ascending, somewhat spreading branches form a large bush up to 18 dm high and 15 dm across (fig. 14).

One form of *Opuntia rufida*, which is here named *O. rufida* var. *tortiflora*, has short-obovate to elliptic joints, relatively remote areoles, and outer perianth segments which are swirled in imbrication and twisted sideways in anthesis (fig. 15). In contradistinction, the typical form has obovate to long-obovate joints, areoles not as distant and outer perianth segments not swirled in imbrication nor twisted on the flower.

Flowering of both forms occurs in April. Fruits require a long period to mature and were not observed.

13 Opuntia rufida var. tortiflora var. nov.

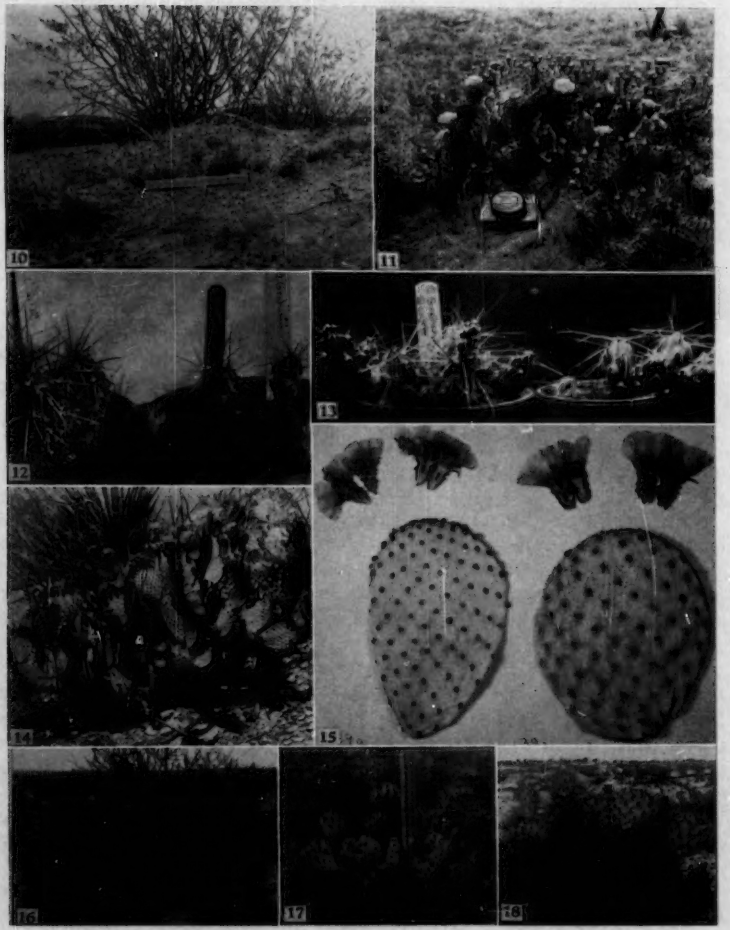
Articulis ellipticis breviter obovoideis; areolis remotis; segmentis perianthii exterioribus tortis. Specimen typicum ex loco dicto "Hot Springs, Big Bend National Park" siccatum conservatum est sub numero 39c, in Herb. Univ. Mich.

Plant large, bushy, 9-18 dm high, 7.5-15 dm wide, occasionally with definite trunk 15 cm high, 10 cm in diameter; branches ascending, somewhat spreading; roots fibrous; joints short-obovate, elliptic to short oval, 13-24 cm long, 10.5-14 cm wide, up to 11 mm thick, pale blue-green to gray-green, purple around areoles; areoles remote, 10-15 mm apart, long elliptic, less elevated and prominent than in type form, to 3 mm long, becoming worm-like in age; wool pale tan, becoming darker; glochids rufous; flower bud with segments swirled in imbrication; flower 3.5 cm long, 5.5 cm across with perianth segments in 4 whorls, outer segments reddish bronze with green trace, long-lanceolate, narrow, twisted, inner segments yellow, fading to pink with tan base; obovate, mucronate, up to 3.5 cm long and 2.3 cm wide; filaments 13 mm long; style yellow, 6 mm in diameter, 23 mm long, stigma lobes 8, green; ovary oblong, up to 2.4 cm long and 1.5 cm in diameter with large, closely set areoles; fruits and seeds not observed.

Collections.—BREWSTER CO.: Big Bend National Park: with Larrea-Agave among igneous rocks, south slope of Chilicotal Mt., 4100 ft., Apr. 3, 1947, No. 16; (type specimen) with Larrea-Agave on steep limestone slopes n.w. of Hot Springs, 2000 ft., April 18, 1947, No. 39c, (d) and (e); with Larrea-Agave on steep n.w. slope of hill e. of Boquillas, 2000 ft., Apr. 11, 1948, No. 237; with Dasylirion-Agave on slopes of brown limestone hills just s. of Dagger Flats, Aug. 2, 1948, No. 899.

14 OPUNTIA TORTISPINA Engelmann, Pac. RR. Rep. 3:41. 1856

Distribution: GENERAL.—South Dakota, Minnesota, Missouri, Nebraska, Kansas, Wisconsin, southeastern Colorado, eastern Arizona, eastern and southeastern New Mexico, Arkansas, and Texas. Established and slowly spreading east of Cincinnati, Ohio (E. T. Wherry, 1922). LOCAL.—Common in grassland and woodland associations in northern Brewster and Presidio counties, also in Jeff Davis County, at altitudes from 3800 to 6700 feet.



Figs. 10-18.—10. *O. schottii* at base of creosote bush, Big Bend National Park; 11. *O. tortispina* in flower (joints less spiny than usual) with grassland vegetation in Del Norte Mountains; 12. Tubercle size as well as number and shape of spines can be compared between *O. schottii* (left) and *O. grahamii* (right); 13. *O. grahamii* x *schottii* with intermediate tubercle size and spine form; 14. *O. rufida* in flower, Big Bend National Park; 15. *O. rufida* var. *tortiflora* (right) contrasted with typical form (left); 16. Note the closely-set areoles of *O. strigil*, east of Ft. Stockton; 17. *O. pottsii* in fruit, with short grass association; 18. *O. azurea* with creosote-lechuguilla association, in Big Bend National Park.

The twisted habit of the spines is well emphasized in the name of this species. The typical form is very distinct with spreading, much-branched habit; long obovate joints which are wrinkled when young; new spines of striking burnt-yellow color, long central spines with shorter, deflexed radials; and characteristically rose-purple fruits (fig. 11). Atypical forms of *O. tortispina* are most likely to be confused with *O. phaeacantha*, but can be identified by more closely set areoles and dense tufts of conspicuous orange-red glochids.

Flowers are borne in profusion commencing about mid-May and continuing into mid-July. The abundant fruits ripen in a month and are filled with juicy pulp and abundant seeds, which have a wide beakless aril.

15 OPUNTIA STRIGIL Engelmann, Rep. U.S. & Mex. Bound. Surv. II, Pt. 1, p. 47. 1859

Distribution: GENERAL.—West of the Pecos River in Texas. LOCAL.—South and east of Ft. Stockton on limestone hills, Pecos County, at altitude from 2600 to 3000 feet.

The meaning of this specific epithet is more obscure than most. The Latin means either "a scraper" (instrument for scraping the skin as after a bath) or "one of a group of undulating flutings in Roman architecture." Perhaps it is a misnomer, meant to be "strigosus" N.L., which, botanically, means "set with stiff bristles."

At a distance the plants look very much like *O. rufida* with densely branched, spreading-ascending habit, short trunk, short-obovate joints, and closely-set but large areoles filled with conspicuous glochids. However, closer inspection shows a very spiny joint, truly one of the most viciously armed species among the Opuntiae under consideration here (fig. 16). Old joints may reach a length of 19 cm and a width of 16 cm.

Flowers, borne in abundance along the upper margin of the pads in early April, measure about 6 cm long and 7 cm wide, with perianth markedly longer than ovary. The fimbriate inner segments are pale lemon-yellow, tinged with pink at the base. Mature fruits, dry, and a rose-purple to plum color, were collected early in July. Seeds which have a narrow beakless aril, are very abundant.

This species forms a monotypic Series (Strigiles) and with its lack of variability is easily identified by the relatively large, thick joints; red and yellow spines which are mostly deflexed; and small, bristly fruits.

Although *O. strigil* is very abundant west of Pecos River in Terrell County and on limestone ridges south and east of Fort Stockton in Pecos County, it was not found in the three Big Bend counties although similar habitats are available. It is included in this discussion because so little information is elsewhere available for it and because of the problem it presents in range of distribution.

16 OPUNTIA POTTSII Salm-Dyck, Cact. Hort. Dyck. 1849. 236. 1850

Distribution: GENERAL.—Southern New Mexico, Trans-Pecos Texas, to central Chihuahua in Mexico. LOCAL.—Occasional in grassland associations of Brewster, Jeff Davis and Presidio counties, at altitudes from 3000 to 6000 feet.

This specific epithet honors John Potts, an official in Chihuahua, who sent cacti to Royal Botanic Gardens, Kew between 1842 and 1850.

One of the least conspicuous of the Platyopuntiae, *O. pottsii* is strikingly different from any other of the region because of its large, tuberous, milky-juiced roots and orange-red flowers, which appear in the middle of May. Joints are highly variable in form, being orbicular, obovate or sometimes almost triangular in shape. A plant rarely bears more than six to eight joints (fig. 17). There are usually one or two long, twisted, spreading spines and one shorter, deflexed spine from each areole along the upper margins of pads, although some spineless joints are found. Mature fruits, collected from late August to October have a distinctive long-pyriform shape and a glaucous, pink-purple color. Seeds are about 6 mm in diameter with a wide beaked aril.

17 OPUNTIA SETISPINA Engelmann in Salm-Dyck, Cact. Hort. Dyck. 1849. 239. 1850

Distribution: GENERAL.—Western Texas, to western Chihuahua in Mexico. LOCAL.—Grassland associations of northern Brewster County, at altitudes from 2400 to 5000 feet.

The relatively thin, acicular spines explain the name "setis" (L. bristle) "spina" (L. spine).

This grassland and encinal species resembles *O. macrocentra,* but has thicker, usually orbicular, joints, and downward-spreading spines (fig. 19). Some specimens also resemble *O. tenuispina* in having noticeably acicular spines, but the latter has a more creeping habit, usually long-obovate joints, fewer and less flattened spines, and the spines mostly restricted to marginal areoles. Joints of *O. setispina* are often curved, making it difficult to slice them for herbarium specimens, and may reach a size of 25 cm in length and 17 cm in width. Generally 2-4 brown spines are borne in an areole, although there may be as many as ten. Of these, one is long and porrect, two are shorter, twisted and porrect, and one still shorter is always deflexed.

When plants of *O. setispina* are in flower, from the middle of May to the middle of July, one notices particularly the very numerous and minute areoles on the somewhat tuberculate ovaries. Flowers are about 6-7 cm long and 6 cm wide; perianth segments are yellow, grading into rose at the base. Fruits begin to mature by late June; occasionally two and even three fruits will develop fused together although the plant appears otherwise normal. No flowers with this tendency were found. Seeds within these atypical fruits are perfectly normal and well formed with a wide beaked aril.

18 OPUNTIA TENUISPINA Engelmann Rep. U.S. & Mex. Bound. Surv. II., Pt. I., p. 50. 1859

Distribution: GENERAL.—Arizona, Zion National Park in Utah, New Mexico, southwestern Texas, northern Chihuahua in Mexico. LOCAL.—Frequent in desert life belt in southern and eastern Brewster County, frequent in encinal belt of Chisos Mountains and Nine Point Mesa, occasional in grassland belt in northern Brewster County at altitudes from 2200 to 5100 feet.

The species name refers to the slender spines which characterize these plants. The cluster typically consists of one very long spine, sometimes deflexed; 1-2 shorter, twisted spines, spreading-deflexed; and one very short deflexed spine. With a low, spreading habit (fig. 20), long-obovate joints (sometimes 27 cm long and 13 cm wide), spines in upper areoles only, and

usually 1 to 3 terete spines per areole, the species resembles *O. phaeacantha* and can only be well distinguished by thinner joints and fewer spines per joint. Low bushes of *O. engelmannii* also may be confused with *O. tenuispina,* but the former have larger areoles and flatter spines. Flowers, bearing yellow segments with a faint rosy blush at the base, appear in early June but are very sparse so are of little use in field identification. A few mature fruits were collected by early August; the seeds have a wide, slightly beaked aril.

19 OPUNTIA MACROCENTRA Engelmann Rep. U.S. & Mex. Bound. Surv. II, Pt. I, p. 292. 1859

Distribution: GENERAL.—South central and southeastern Arizona, southern New Mexico, western Texas, Chihuahua in Mexico. LOCAL.—Occasional in grasslands and common on desert flats in Brewster and Presidio counties, from 1900 to 4800 feet.

The name "macrocentra" means large central spines, a feature which immediately distinguishes this species in its typical form. Only the uppermost areoles of a joint bear spines; three or four are usually present per areole. There is at least one spine longer than the two intermediate ones; and one, lower in the areole, is very much shorter and deflexed. The species is well segregated from *Opuntia phaeacantha* by thinner and usually orbicular joints, slender leaves, smaller and more closely set areoles, lack of bristles, more acicular spines, and more elongate flowers with narrower outer segments. *O. setispina,* alike in orbicular joints, closely-set areoles, and large flowers, always has thicker joints with spines spreading downward, while *O. macrocentra* has porrect, upward-spreading spines although, in sheltered habitats, individuals are frequently spineless. Young joints are a beautiful reddish- or blue-green. Mature joints have a tendency to become purple, especially during sunny summer months and in dry years; in size they may reach a length of 26 cm and a width of 17 cm. There is also a marked tendency for pads to be twisted.

O. macrocentra is one of the earliest cacti in the region to begin flowering; buds open from April to the middle of May. Flowers may be almost as long as the joints and sometimes the perianth is twice as long as the ovary. Inner perianth segments are pale to dark yellow with rose bases and white tips. The many fertile fruits ripen by early July; seeds are large with a wide, beakless aril.

20 **Opuntia macrocentra** var. **minor** var. nov.

Diffusa; paucis ramis erecte ascendentibus; articulis quam in forma typica minoribus breviter obovatis; areolis remotioribus; spinis 2-7, varie divergentibus; floribus fructibusque ignotis. Specimen typicum ex loco dicto "Ruidosa, Presidio Co., Texas" siccatum conservatum est sub numero 1081, in Herb. Univ. Mich. et vivum conservatum est sub numero 19607 in Hort. Mich.

Plant mostly spreading, much branched; some branches vertically ascending; trunk absent; roots fibrous but sometimes with fleshy taproot; joints short obovate, from 6 cm long and 5 cm wide to 10 cm long and 7 cm wide, to 8 mm thick, heavily glaucous, young joints blue-green, older joints glaucous green; leaves subulate, apiculate, 4-6 mm long, 1.5 mm wide, green; areoles 15-20 mm apart, large, ovate to circular, 3-6 mm long, 2-4 mm wide, becoming larger in age; wool tan to gray; spines 2-7 (mostly 3-4), from areoles on upper half of joint, acicular, twisted, angular, young spines rufous below, be-

coming white with orange tips, older spines rufous with orange tips, finally becoming all brown; 1-3 spines longer, mostly 4.5 cm, a few to 6 cm long, spreading, 1-4 spines shorter, mostly 2.5 cm, spreading, 1 spine short, 2.2 cm, always deflexed, rufous below, white toward tip; bristles absent; glochids abundant, conspicuous, bright orange when young, yellow and rufous with yellow bases and to 12 mm long in older areoles; flowers unknown.

Type locality: With Larrea on sandy soil 1.4 miles southeast of Ruidosa along road to Presidio, Presidio County.

Distribution: With Larrea and Larrea-Prosopis associations on sandy flats along the Rio Grande, from 2100-2700 feet, Ruidosa to Presidio, Presidio Co., and north of Santa Elena Canyon in Big Bend Nat. Park, Brewster County.

The spreading branches of this small-jointed and very spiny variety form an extensive clump among the creosote bushes; occasional erect branches, three to four joints long, reach a height of about 3 dm (fig. 21). All spines are rufous, unlike those of the typical *O. macrocentra* with the terminal half paler or white. Tap roots on one plant were definitely fleshy. Neither flowers nor fruits were found.

PRESIDIO CO.: (Type specimen) with Larrea on sandy flats, 2700 ft., 1.4 mi. from Ruidosa along road to Presidio, Aug. 26, 1948, No. 1081. BREWSTER CO.: With Larrea-Prosopis on sandy soil, 4.8 mi. n. Ste. Elena Canyon, 2200 ft., Big Bend National Park, Sept. 16, 1948, No. 1211.

OPUNTIA sp.

Two plants were found (fig. 30) that closely resembled *O. macrocentra* with a few long spines in each areole along the upper margin of the joints, but spines were yellow rather than dark reddish-brown, areoles were relatively distant rather than closely set and flowers were yellow throughout. These plants therefore suggested hybridization between *O. lindheimeri* and *O. macrocentra*. Continued observation of specimens under cultivation will be necessary to substantiate this hypothesis.

Collections.—BREWSTER CO.: With Bouteloua-Juniperus in valley southwest of Old Blue in Glass Mts., on Victor Pierce Ranch, May 19, 1947, No. 125; on low limestone hill with Pinus-Quercus, Yates Ranch, Glass Mts., June 3, 1948, No. 506.

21 OPUNTIA AZUREA Rose, Contr. U.S. Nat. Herb. 12:291. 1909

Distribution: GENERAL.—Zacatecas and Durango in Mexico, near Rio Grande in Brewster County, Texas. LOCAL.—Locally abundant with Larrea-Agave lechuguilla, on barren limestone ridges one mile northeast of Solis Ranch in the Big Bend National Park, at about 1900 feet.

The specific epithet refers to the blue-green color of the joints. Successive joints of three years' growth show a striking contrast between young creamy-white spines, mature bright yellow spines and the old black spines (fig. 18). In each spine cluster one main spine is longer and porrect, 1-3 are shorter and spreading, and one is very short and points downward. Britton & Rose (1919) describe the spines of these plants as only 2 to 3 cm long and the flowers as fading pink, but in Texas some spines reach a length of 6.3 cm, and flowers fade to white on the second day.

Superficially the species resembles *O. lindheimeri* in spreading and ascending habit and orbicular to short obovate joints with yellow spines, but it

differs in having more closely set areoles, occasional bristles, marked contrast in spine color and yellow flowers with red centers similar to those of *O. macrocentra*. Flowering period lasts from early to late April. Mature fruits were not available.

Plants were found only in a small colony at this one station.

22 OPUNTIA PHAEACANTHA Engelmann in Gray, Mem. Amer. Acad. 4:52. 1849

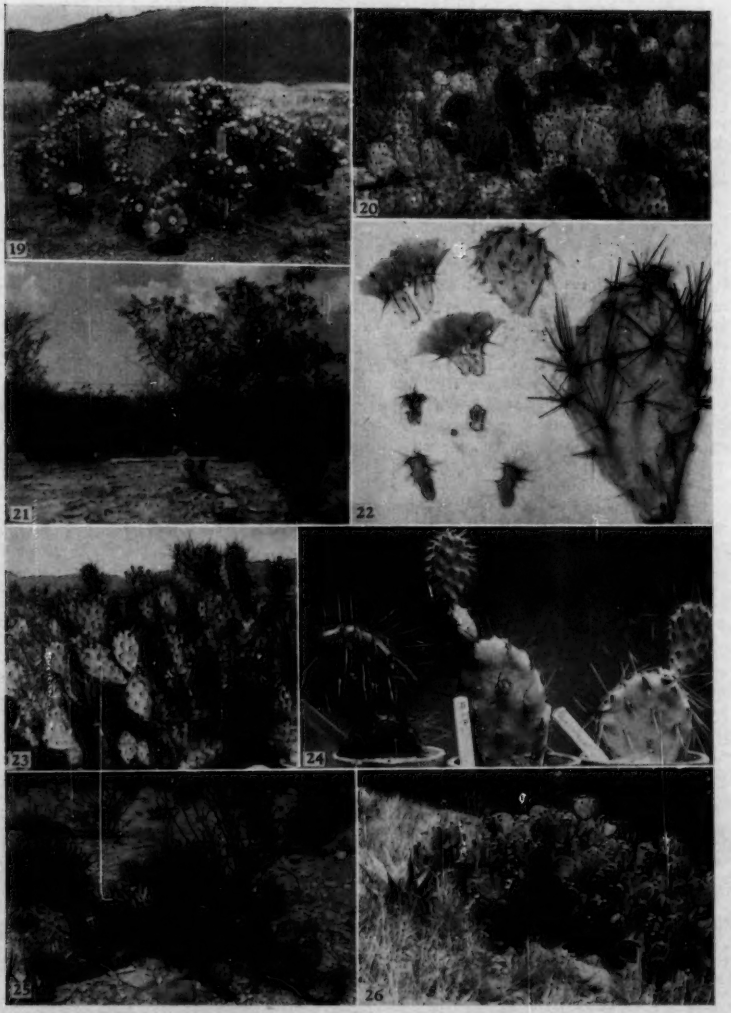
Distribution: GENERAL.—California, southern Utah, Arizona, southeastern and western Colorado, New Mexico, western Texas, and in Chihuahua, Mexico. LOCAL.—In desert shrub, arid grassland and encinal belts of Brewster, Jeff Davis and Presidio counties at altitudes from 1600 to 5500 feet.

"Phae" (Gr. brown) and "acantha" (Gr. spine) constitutes an apt name for this reddish brown-spined common species of the southwest.

Usually a low, spreading bush, but extremely variable in most characteristics, *Opuntia phaeacantha* is one of the most difficult species in the Big Bend to identify with certainty. Flowers and fruits are too sparse to be of much help either. After study in the field, many distinct forms of the species can be recognized, each differing in subtle variations of habit, spine number, and spine arrangement, but intergrading to defy definition. Under cultivation many of these differences become less evident. Therefore, the group is here broadly defined, ranging from spreading plants with a few spines in the marginal areoles, to larger, more ascending bushes reaching 15 dm in height (with a short thick trunk) and with very spiny joints (fig. 25). Occasional joints reach 30 cm in length and 19 cm in width but average joints measure 10 to 22 cm long and 9 to 15 cm wide. Thickness of joints on different individuals varies from 7 mm, which is relatively thin for the Opuntiae, to 15 mm, which is relatively thick. Bristles are consistently present in some forms and absent in others. Three to four spines constitute a cluster, although there may be as many as ten in an areole. One to four are long, others are shorter and spreading, one is much shorter and deflexed. Although the color pattern is similar to that in *O. macrocentra*, flowers of *O. phaeacantha* are characteristically shorter with a stouter ovary. Other differences in floral structure include a short thick style, usually bulbous at the base rather than above it; stigma lobes short and heavy instead of long and thin; outer perianth segments broadly conic; perianth no longer than ovary and frequently shorter; areoles distant on the ovary; and flowers fading to a pale tan color, rather than pink as in *O. macrocentra*. Flowers are sparse and open from early April to early July. Mature fruits with abundant seeds were collected from the middle of July on. Seeds have a very wide beakless aril.

23 **Opuntia spinosibacca** sp. nov.

Robusta, diffusa, plerumque erecta; ramis adscentibus; radicibus fibrosis; saepe basi caule sublignoso teretique; articulis planis, longi-obovatis, basi attenuatis, superficie paullum tuberculatis, glaucis, viridibus, ad areeolas purpureis; areolis ellipticis, remotis, magnis, fulvilanosis et seta colore flavida vel rufida gerentibus, plerisque armatis; spinis 2-5, validis, teretibus, superioribus ascendentibus divergentibus, inaequalibus, junioribus albidis, rufescentibus, aetate griseinigris; aliis inferioribus lateralibus 1 vel 2 setosis, deflexis, griseis, longis, conspicuis; infima brevi, deflexa; pallida floribus 5.5 cm longis, 5 cm latis,



Figs. 19-26.—19. *O. setispina* in flower, with short grass association, east of Alpine; 20. *O. tenuispina*, west of Sanderson; 21. *O. macrocentra* var. *minor*, with creosote bush on sandy soil along Rio Grande River; 22. *O. spinosibacca* in Big Bend National Park. Note spiny ovary and fruits; 23. *O. spinosibacca*—note tubercles on joints; 24. Fruit of *O. spinosibacca* (center) proliferating to form new joint, pads of the closely related *O. phaeacantha* to left and right); 25. *O. phaeacantha* on desert flats with creosote bush, east of Santiago Mountains; 26. *O. lindheimeri* var. *chisosensis* with pinyon-oak-juniper association in Chisos Mountains.

flavis, intus rubellis, segmentis perianthii 5-seriatis, exterioribus obovatis, longe-apiculatis, interioribus spatulatis; filamentis flavis; stylo flavo, stigmatis lobis 7, flavidi-viridibus; ovario obconico, areolis magnis, remotis, setis flavidirufis, superioribus areolis 1-3 spinas valides albas, basi rufas, gerentibus; bacca immatura succosa, matura sicca, etuberculata, longe oblonga, prolifera, areolis superioribus 1-4 spinas validas et albas gerentibus; seminibus magnis, 6 mm diametro, commissura lineari distincta, late marginatis. Specimen typicum ex loco dicto "Boquillas, Big Bend National Park, Brewster County, Texas," siccatum conservatum est sub numero 236 in Herb. Univ. Mich. et vivum conservatum est sub numero 19109 in Hort. Mich.

Plant a tall, massive bush, to 15 dm high, and 18 dm wide; trunk sometimes present, to 6 dm high, 18 cm in diameter; branches ascending, slightly spreading; roots fibrous; joints obovate to long ovate with attenuate base, 10-24 cm long, 7.5-11 cm wide, 7-12 mm thick, heavily glaucous, green with purple around areoles; texture dry, granular; leaves long subulate, mucronate, green to pink with bronze tips; areoles elevated on small protuberances, relatively distant, 30-40 mm apart, oval, large, to 6 mm in length and 3 mm in width; wool tawny or gray; spines 2-5, from all but lowermost areoles, subulate, mostly elliptic in cross-section, slightly twisted, young spines white with rufous bases, older spines reddish orange to dark reddish-brown with paler tips, finally becoming gray in age, 1-4 spines 3.5-7 cm long, porrect, spreading, 1 spine from base of areole, only to 2 cm long, much deflexed, gray; bristles 2, deflexed from base of areole, rufous or gray, to 1.2 cm long; glochids in upper margin of areole, yellow to rufous, 4-7 mm long; flower about 5.5 cm long and 5 cm across with perianth segments in 5 whorls, outer segments with yellow margins, pinkish-green trace, obovate, long-apiculate, inner segments yellow with red base, long obovate, apiculate, to 2.5 cm long and 1.8 cm wide; filaments yellow, to 11 mm long, anthers white or yellow; style white or yellow, bulbous above base, 18 mm long, stigma lobes 7, yellowish-green, 4 mm long; ovary tuberculate, obconic with tapering base, reaching 3 cm in length and 1.5 cm in diameter, with relatively large and distant areoles, uppermost ones bearing subulate, apiculate leaves, dense tan wool, numerous yellow to rufous glochids and 1-3 subulate spines, rufous below, white above; fruit becoming dry, shrunken, tuberculate, capable of proliferation or transformation into joint, long-oblong, with truncate base, to 3.5 cm long and 1.5 cm in diameter when mature, glaucous, pale purple with distant areoles, long yellow or orange glochids, areoles on upper half with 1-4 rufous and white subulate spines; umbilicus v-shaped, 10 mm deep; flesh dry, granular, cream colored; seeds few per fruit, large, rough (noticeable angle between body of seed and aril) yellow with green embryo, beakless, deeply notched at hilum, reaching 6 mm in diameter, 2 mm in thickness, aril 1-1.5 mm wide.

Type locality: On slopes of limestone hill just west of ranger's quarters, Boquillas, Big Bend National Park, Brewster County, Texas.

Distribution: Locally abundant around Boquillas, especially on rocky slopes from Boquillas west half way to Hot Springs, in Larrea-Agave association on limestone formations.

The species name is given to emphasize the very distinctive spiny fruits. The most striking features are markedly ascending branches, reaching 15 dm in height; protuberances elevating each areole on the joint; spiny ovaries; and tuberculate, dry, and spiny fruits (figs. 22 and 23).

In the key by Britton & Rose (1919) these characteristics bring it into the series Phaeacanthae near *O. angustata* and *O. phaeacantha*. *O. angustata* differs in having shorter, more or less white spines, and no mention of tuberculate joints or dry tuberculate fruits. *O. phaeacantha* agrees in having somewhat conspicuous bristles, reddish spines and similar flowers, but differs in its more spreading habit, short-obovate to orbicular non-tuberculate joints, and juicy, non-tuberculate, naked fruit.

Flowering period extends from April to about the middle of May, with fruits maturing a month after the flowers. Fruits are mostly sterile and readily

proliferous (fig. 24). A few seedlings with very long (to 6.5 cm) white to reddish brown spines were found near the parent plants.

Collections.—Big Bend National Park, BREWSTER CO.: Locally abundant with Larrea-Agave, and *Jatropha spathulata*, at 2250 ft., on rocky limestone slopes e. of rangers' headquarters at Boquillas, Apr. 17, 1947, No. 36; Apr. 11, 1948, (type specimen) No. 236, No. 238, No. 241, No. 243:

24 OPUNTIA ENGELMANNII Salm-Dyck in Engelm., Bost. Jour. Nat. Hist. 6:207. 1850

Distribution: GENERAL.—Southeastern Arizona, southern New Mexico, western Texas, and Mexico, in Chihuahua, Durango, Nuevo Leon and Sonora. LOCAL.—Grassland and desert associations throughout Brewster, Jeff Davis and Presidio counties, at altitudes from 2100 to 6700 feet.

This large and well-known prickly pear is deservedly named after one of the earliest and greatest authorities on cacti, (particularly those from the Trans-Pecos region), Dr. George Engelmann, who worked on the many specimens sent to him by early biologists with the government surveys.

This species is the least restricted and most abundant cactus in the Big Bend area. It usually occurs as a massive bush with short thick trunk, and large heavy pads, although low spreading forms are encountered. Joints, especially on plants in the Chisos Basin of the Big Bend National Park, have a tendency to expand in three planes—a possible reversion to cylindrical form. This tendency was also evinced on one specimen of *O. macrocentra* and one of *O. lindheimeri* (fig. 29). Joints are extremely variable in shape, ranging from elliptic through long-obovate or orbicular, to reniform, and in size from 10.5 to 45 cm long, 10.5 to 33 cm wide, and 6-40 mm thick. Spines may be entirely lacking, or present only in a few areoles, or present in all but the lowermost areoles. Typically in each cluster there are 2-3 long, and 1-3 shorter, flattened, somewhat deflexed spines; 1-2 deflexed bristles are often present also.

Flowering is prolific from late April in the desert belt to late July in the arid grassland belt. Flower color ranges from clear yellow and yellow heavily streaked with orange, to yellow segments with rose bases; stigma lobes are yellow to green. Mature, almost naked, fruits are formed by the middle of May and are eaten by many animals. Seeds are relatively small with a narrow beakless aril. Seedlings are easily identified in the field by the hairy bases. Hairs are also present in lowermost areoles of the first young pads and in areoles on trunks of mature plants.

25 Opuntia engelmannii var. wootonii (Griffiths) nov. comb. (*O. wootonii* Griffiths, Rep. Mo. Bot. Gard. 21:171. 1910.)

Plant somewhat ascending, to 6 dm high, spreading to 12 dm wide; trunk absent; branches much subdivided; roots fibrous; joints long-ovate or obovate, occasionally attenuate at both ends, 14.5-25 cm long and 10-15 cm wide, relatively thin, 6-8 mm thick, heavily glaucous; texture granular; areoles distant, 30-40 mm apart, short ovate, large, to 10 mm long and 7 mm wide; wool pale tan; spines 4-7, from areoles on upper 2/3 to 4/5 of joint, subulate, twisted, young spines mostly black with paler tips, older spines pinkish-white with reddish black bases and horny yellow tips, becoming red throughout when wet, finally becoming grayish-black, annulately marked; 1 spine very long, to 7.3 cm usually flattened, porrect or spreading downward, 2-3 spines shorter, to 5.5 cm long, elliptic to flattened, twisted, spreading, 1 spine very short, to 2.3 cm long.

elliptic, deflexed; bristles 0-2, white with yellow or orange tips, reaching 5 mm in length; glochids yellow, orange, or reddish-brown; flower and fruit not observed.

Type locality: Organ Mountains of New Mexico.

Distribution: Scattered in desert shrub vegetation of Tornillo Flats and locally abundant in Christmas Mountains.

From collections made by Prof. E. O. Wooton in the Organ Mountains of New Mexico, Griffiths (1908) described *O. wootonii* as a new species. Britton & Rose (1919) subsequently delegated this name to synonymy under *O. engelmannii*. Unlike the plants in the original description with joints attenuate at both ends, these Texas representatives have mostly obovate joints which are only occasionally attenuate at the base (fig. 28).

In contrast to the typical *O. engelmannii* with its massive habit, mostly orbicular joints, and markedly flattened spines reaching about 5 cm in length, this variety has a more spreading habit, elongate-obovate joints and conspicuous long white spines, reaching 7.3 cm in length and little flattened. Spines have a white bloom which is easily penetrated by water so they darken to red when wetted by rain.

An extensive population is well established on desert plains within the Christmas Mountains. A few scattered specimens were found elsewhere, almost always with creosote-mesquite association, so it is probable that local edaphic conditions of greater moisture have contributed to development of this race.

It may represent a separate evolutionary development along parallel lines to the plant of the Organ Mountains, possibly disjunct and never part of the same population. Nevertheless, one hesitates to give it a distinct name on a chiefly geographic basis. If it is too conservative to consider the Big Bend population as essentially the same as Griffith's *O. wootonii*, the most important matter is to point out the existence of similar evolutionary trends in isolated areas. It will be interesting later to cultivate them side by side and to hybridize them.

Collections.—BREWSTER CO.: With Prosopis on sandy clay, 1900 ft., near Solis Ranchhouse along Rio Grande, Big Bend Nat. Park, April 28, 1948, No. 274; with Larrea-Flourensia and *Agave lechuguilla*, 3200 ft., in Dagger Flats, Big Bend Nat. Park, Aug. 2, 1948, No. 873; with Larrea-Prosopis 12 mi. n. of Terlingua on road to Alpine, Sept. 14, 1948, No. 1182; with Larrea-Prosopis, 2900 ft., just n.e. of Terlingua, Sept. 17, 1948, No. 1224; with Prosopis, 4.1 miles along road into Christmas Mts., n.e. of Study Butte, Sept. 18, 1948, No. 1231; with Larrea-Prosopis on flat valley in Christmas Mts., Sept. 18, 1948, No. 1236; with Larrea-Prosopis, near end of road in Christmas Mts., Sept. 18, 1948, No. 1244.

26 **Opuntia engelmannii** x **phaeacantha** hybr. nov.

Magnitudine parentibus similis; areolis remotis, elevatis, plerisque armatis; spinis 2-5, subcompressis, subdeflexis, retrorsum divergentibus, junioribus spinis subnigris, rufescentibus floribus, flavis, intus rubellis, fructibus longis, obovoideis seminibus magnis, late marginatis. Specimen typicum ex montibus dictis "Glass Mountains, Brewster Co., Texas" siccatum conservatum est sub numero 113 in Herb. Univ. Mich. et vivum conservatum est sub numero 18906 in Hort. Mich.

Plant a low spreading bush, attaining a height of 7.5 dm and a width of 18 dm; trunk rarely present; branches only slightly ascending; roots fibrous; joints orbicular, obovate or ovate, 15-45 cm long, 12-40 cm wide, 7-13 mm thick; glaucous, purple around areoles; texture granular; leaves subulate, with curved tip, mucronate, 5-15 mm long, 1-3 mm

wide, green to purplish-pink; areoles relatively distant, 30-45 mm apart, elevated, prominent, oval, elliptic to orbicular, large, 9-10 mm long, 4-7 mm wide; wool abundant, tan or reddish-brown, becoming gray in age; spines 2-5 from areoles on upper 2/3 to 4/5 of joint, especially along edge, subulate, more or less flattened, twisted, sometimes curved, young spines white or reddish-brown, with black bases and orange tips, older spines reddish-brown, or more often black, with orange, or reddish-brown tips, finally becoming gray and 7-8 per areole, 1 spine longer, reaching 5.1 cm in length, terete, porrect, 2 spines shorter, 2.5-3 cm long, spreading, 1 spine very short, 1.7-2.5 cm long, white or gray, flattened, usually deflexed; bristles 0-2, spreading, gray, to 7 mm long; glochids abundant, long, scattered in areole, orange when young, yellow, orange or dark reddish-brown with yellow bases in older areoles, finally becoming gray and 17 mm long; flower reaching 7.5 cm in length and 6 cm across, with perianth segments in 4 whorls, outer segments green with pinkish tip and yellow margins, obcordate, inner segments bright yellow sometimes with pink to red bases, short obcordate, emarginate, slightly fimbriate; filaments mostly green, sometimes yellow or white above, 11-14 mm long, anthers yellow; style white to pinkish, to 5 mm thick just above base and 19 mm long, stigma lobes 6-10, pale green, or yellowish green, 4.5 mm long; ovary long conic, curved, 3-4.5 cm long, 1.5-2.3 cm in diameter, with distant, small areoles bearing a few subulate leaves, yellow or reddish-brown glochids and a few bristles; fruit purple, long obovate, reaching 3.5-5 cm in length and 2.5 cm in diameter, with small, distant areoles bearing few glochids and no spines; umbilicus v-shaped, 5 mm deep; seeds yellow, rough, irregularly-shaped, beakless, deeply notched at hilum, large, 6 mm long, 4.5 mm across, 2 mm thick, aril 1 mm wide.

Type locality: Low limestone hill on Victor Pierce Ranch, just west of Glass Mountains, Brewster County, Texas.

Distribution: Culberson, Pecos, and Val Verde counties, desert shrub, arid grassland and encinal belts in Brewster and Presidio counties at altitudes from 2600 to 4400 feet.

Flowers, fruits and seeds of this hybrid most closely resemble the *O. phaecantha* parent but the massive habit, orbicular joints, somewhat elevated and distant areoles, and flattened spines suggest *O. Engelmannii* (fig. 27). Young spines are usually darker than those of either parent; perhaps an instance of interacting genetic factors, one derived from each parent.

The hybrid shows little restriction in distribution since the parents are themselves common throughout the region but it is found more frequently in the Glass Mountains and grassland areas of Brewster County than in the desert shrub life belt.

Collections: BREWSTER CO.—With Juniperus on low limestone hill, 4400 ft., Victor Pierce Ranch, just w. of Glass Mts., May 13, 1947, No. 112 (type specimen) No. 113; with Larrea-Agave, on limestone hill n. of Terlingua, 3000 ft., May 9, 1948, No. 326; with Juniperus and grass, in Santiago Mts., 4000 ft., along rd. to Marathon, May 9, 1948, No. 340; with Bouteloua-Juniperus, on Sohl Ranch, w. of Del Norte Mts., May 22, 1948, No. 448; in draw with *Juglans rupestris* along rd. from Rt. 67 in to Gilliland Canyon, Glass Mts., June 4, 1948, No. 508; with Yucca, Agave and other desert shrubs on slopes of chert cuesta, Pena Blanca Mts., s.e. of Marathon, July 8, 1948, No. 727; with Larrea-Leucophyllum along Chalk draw, n. of Nine-Pt. Mesa, Aug. 3, 1948, No. 912; with Larrea-Flourensia on flat, 20 mi. n.e. from Reagan Canyon on Bullis Gap rd., Aug. 17, 1948, No. 1012; with Larrea-Agave and Fouquieria, on north slope, Christmas Mts., Sept. 18, 1948, No. 1241; with Larrea-O. leptocaulis, 3400 ft., on sandy flat, s. of Nine-Pt. Mesa, Sept. 26, 1948, No. 1270; CULBERSON CO.—With Yucca-Agave, 4½ mi. w. of Van Horn, Aug. 8, 1948, No. 942. PECOS CO.—With Juniperus on limestone hill, 15 mi. s. of Ft. Stockton, July 3, 1948, No. 694; with Bouteloua-Prosopis, 13½ mi. w. of Sanderson, along Rt. 90, July 9, 1948, No. 744. PRESIDIO CO.—With Prosopis on sandy flat, 2600 ft., 8½ mi. s.e. of Ruidosa on rd. to Presidio, Aug. 26, 1948, No. 1083, No. 1084. VAL VERDE CO.—With Prosopis on overgrazed rangeland, 31 mi. n.w. of Del Rio, Mar. 31, 1948, No. 201.

27 OPUNTIA LINGUIFORMIS Griffiths Rep. Mo. Bot. Gard. 19:270. 1908

Several large bushes of this species have become well established near an abandoned Mexican dwelling about one mile north of the mouth of Tornillo Creek, at an altitude of 1800 feet, in the Big Bend National Park (fig. 5). It seems probable that the plants will eventually become a part of the natural vegetation, at least in the mesquite thicket along the creek. There is also the possibility of spontaneous crossing in course of time which may inaugurate a new population. Since this species has only been recorded as native around San Antonio, Texas, and is not listed by Bravo (1937) in Mexico it is remarkable to find it thriving so far afield. Flower buds were forming early in April but neither flowers nor fruits were obtained.

28 OPUNTIA LINDHEIMERI Engelmann, Bost. Jour. Nat. Hist. 6:207. 1850

Distribution: GENERAL.—Southwestern Louisiana, reported in southern New Mexico by Tidestrom (1941), southeastern to southwestern Texas, northern Tamaulipas in Mexico. LOCAL.—Rare in grasslands of northern Brewster County and in Jeff Davis County, at altitudes from 2700 to about 6000 feet.

This species honors Ferdinand Lindheimer who collected actively in southeastern Texas from 1843 to 1852.

The spreading-ascending bush closely resembles *O. engelmannii*, but is distinguished by circular to elliptic areoles, consistently yellow spines, and lack of bristles in areoles (fig. 29). Joints are of variable shape, degree of spininess, and size but rarely become larger than 33 cm in length and 24.5 cm in width. When present the flattened, curved, reddish-brown to yellow spines appear in clusters with 1-4 longer and spreading downward and 0-2 spines which are lower in the areole, shorter and usually deflexed.

Flowers, appearing from the middle of May to early June, are large (7.5-9 cm long and up to 7 cm wide). Naked fruits ripen within about six weeks and are as prolific, juicy and edible as those of *O. engelmannii*. They may reach a length of 7 cm and 4 cm in diameter.

Many specimens were noted from San Antonio, west to Del Rio and north to Devil's River, but further west toward the Pecos and beyond, *O. lindheimeri* becomes rare and forms less massive bushes.

29 **Opuntia lindheimeri** var. **chisosensis** var. nov.

Robusta; articulis plerisque orbiculatis; areolis obovatis, spinis 1-5 saepe curvatis, paullum compressis; floribus ignotis; fructibus subglobosis, 3.3-4.5 cm longis, 3.5 cm latis; seminibus 5 mm diametro. Specimen typicum ex loco dicto "Basin, Chisos Mountains, Big Bend National Park, Texas" siccatum conservatum est sub numero 810 in Herb. Univ. Mich. et vivum conservatum est sub numero 19606 in Hort. Mich.

Plant a large bush, reaching about 10 dm in height, and 20.5 dm in width; trunk absent; branches spreading and ascending from short, thickened base; roots fibrous; joints usually 6 per branch, mostly orbicular, some short-obovate with attenuate base, 16-29 cm long, 13-22 cm wide, and 6-15 mm thick, heavily glaucous, yellow-green to gray-green; texture mealy; areoles relatively distant, 30-35 mm apart, short oval to circular, 7-8 mm long, 5-6 mm wide, becoming larger and elevated in age; wool abundant, tan; spines 1-5, from areoles on upper 2/3 to all of joint, subulate, elliptic in cross section, often curved, spreading downward, young spines bright yellow with paler tips, older spines all yellow or reddish-orange with yellow bases and yellow tips; 1 spine very long, to 6.7 cm, flattened, 1-4 spines shorter, about 5.5 cm, annulate, curved, spreading; 1 spine very short, to 2 cm, much deflexed; bristles absent; glochids in dense tufts, yellow throughout, to

20 mm long and conspicuous in older areoles; flower not observed; fruit juicy, reddish purple, glaucous, small, short-oblong with truncate base to globose, 3.3-4.5 cm long and 3.5 cm in diameter, with small, inconspicuous, distant areoles bearing only a few yellow glochids; umbilicus saucer-shaped, to 9 mm deep; flesh purple; seeds yellow, beakless, notched at hilum, large, 5 mm long, 4 mm wide, 2 mm thick, aril 1 mm wide.

Type locality: Basin of Chisos Mountains, Big Bend National Park, Brewster County, Texas.

Distribution: Encinal belt in Chisos Mountains, Big Bend National Park, Brewster County, Texas, at altitudes from 5200 feet to 6500 feet.

The varietal name is derived from the type locality in the Chisos Mountains. Bushes are compact, usually less than 10 dm high, and colorful with yellow, sometimes red, spines against a glaucous-green background (fig. 26). The red-spined form is about as common as the yellow-spined but does not occur at as high altitudes above the Basin. A profusion of flowers appear in May and the deep red fruits ripen by the middle of July. Areoles are smaller and less elevated, and spines more spreading, than in the typical *O. lindheimeri* (fig. 29). Unlike the large pyriform fruit of the typical form, fruit of this variety is relatively small and almost globose, with very shallow umbilicus and large seeds.

This variety is the most conspicuous and abundant cactus in encinal and montane belts from Upper Green Gulch all through the Basin and up the slopes of the higher peaks of the Chisos Mountains.

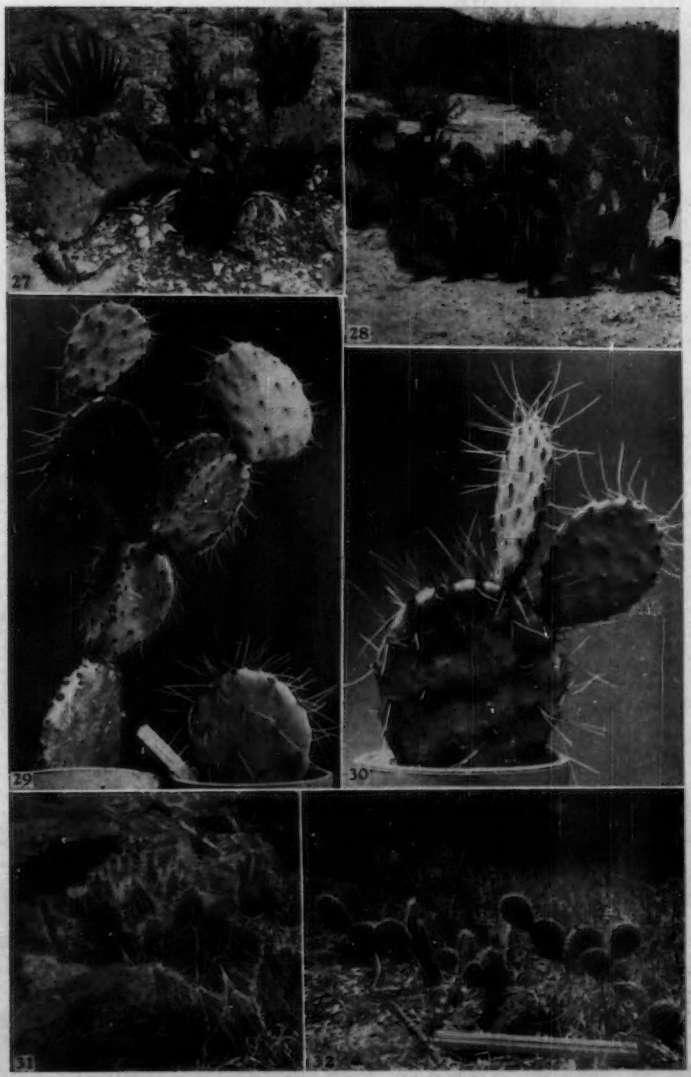
Collections.—Big Bend National Park, BREWSTER CO.—With Quercus-Pinus on very sandy soil, 5500 ft., basin of Chisos Mts., April 8 and July 17, 1948, No. 223 (type specimen) No. 810, No. 811, No. 813; with *Pseudotsuga taxifolia* and *Cupressus arizonica* in Upper Juniper Canyon, near Boot Springs, 6500 ft., Chisos Mts., April 18, 1948, No. 253, No. 254; with Quercus, Staphylea, and grasses, 4400 ft., at Lower Cattail Canyon, evidently washed down from above, May 8, 1948, No. 314; in grassy meadow southwest of Pulliam Peak, 5200 ft., Chisos Mts., July 14, 1948, No. 776; with Pinus-Quercus, along Lost Mine Trail, Chisos Mts., July 15, 1948, No. 791, No. 794.

30 OPUNTIA TRICHOPHORA (Engelmann) Briton & Rose, Smiths. Misc. Coll. 50:535. 1908

Distribution: GENERAL.—Northeastern Arizona, western Colorado, eastern New Mexico, northern Texas, Oklahoma. LOCAL.—In a grassy swale called "Hidden Valley," in hills south of Lane Ranch buildings, at 4900 feet, southwest of Alpine, Brewster County.

The characteristic of bearing ("phora" Gr.) hairs ("Tricho" Gr.) from lower and older areoles clearly distinguishes this species from its close relative, *O. polyacantha* (figs. 31 and 32). Creeping and ascending branches form a clump about 20 cm high and 10 dm in diameter. The elliptic joints are almost obscured by abundant, long, setiform spines which, curving downward, give the plant a shaggy appearance. Old joints become woody and almost terete, with prominent areoles. All areoles are spiniferous with spines numbering from 8-30 or more in each cluster. All are flattened but 2-6 are longer (3-6.5 cm) and twisted; the remainder are about 2-3 cm long. Spines in lowermost areoles often become especially long and flexible. The few yellow glochids are inconspicuous.

The lemon-yellow flowers, opening early in May, are about 6 cm long and 4-5 cm wide. Fruits were not collected.



Figs. 27-32.—27. Immature plant of *O. engelmannii* x *phaeacantha*; 28. *O. tenuispina* (left), *O. phaeacantha* (center) and *O. engelmannii* var. *wootonii* (right) in creosote-tasajillo association, Big Bend National Park; 29. *O. lindheimeri* var. *chisosensis* (right) has less elevated areoles and more spreading spines than the typical form (left). The tendency for occasional Opuntia pads to expand in three directions is seen on the latter; 30. Joints from a possible hybrid, with the long acicular spines in marginal areoles characteristic of *O. macrocentra*, and the yellow spines and remote areoles characteristic of *O. lindheimeri*; 31. *O. trichophora* in flower, with grasses, among igneous rocks, south of Alpine; 32. *O. polyacantha* in a grassy opening in pinyon-oak-juniper association in Davis Mountains.

Previous records had given the most southern, and only Texas station, as El Paso. In the Big Bend the species is very rare, being found only at the locale described above.

31 OPUNTIA POLYCANTHA Haworth, Suppl. Pl. Succ. 82. 1819

Distribution: GENERAL.—Panhandle plains and Davis Mountains of Texas, eastern and northern New Mexico, northern Arizona, southern Utah, throughout Colorado, arid habitats on the plains along the Missouri, northeastern Oklahoma, Nebraska, North Dakota, Montana, Washington, north of the borderline of United States, British Columbia, and Alberta as far north as Peace River. LOCAL.—Occasional in montane belt in Davis Mountains, Jeff Davis County.

This species well earns its epithet of "many spines" and is one of the most distinct of the Opuntiae in the Big Bend Region.

The procumbent plant, with terminal joints and some short branches ascending, forms a clump about 2.5 dm high and 9 dm wide. The obovate joints sometimes reach a length of 15 cm, a width of 11 cm and a thickness of 10 mm. Stem surfaces are somewhat tuberculate with diamond to linear-hexagonal shaped elevations up to 2 mm high. One to eight acicular spines are borne in each areole; usually 1 is longer and may be porrect, 2-7 are shorter, spreading and radial (fig. 32).

Distinguished from the closely-related *O. trichophora* by tuberculate surface; fewer spines, more deflexed in appearance; and the absence of any hairs in basal areoles, *O. polyacantha* is equally rare here and likewise occurs in a montane association in the northern part of the area.

Flowers, which may reach a length of 6.4 cm and a width of 4.5 cm begin to appear in late May. Mature fruits, which are dry and bear 1-6 white bristles in each areole, were collected in the latter part of August. Seeds are the largest among these Opuntiae discussed, measuring 7 mm long by 6 mm in diameter, with a broad beaked aril. Several thriving seedlings were found in the forest litter.

O. polyacantha is of sporadic occurrence in Davis Mountains. W. L. Bray in 1902 collected the species in Limpia Canyon above 6000 feet. J. Ferris also found it somewhere in the Davis Mountains in 1925. L. C. Hinckley has collected material "on Mount Livermore" at 8382 feet and "with *Pinus ponderosa* and *Pinus flexilis*" at about 7450 feet. My only collection was from the north slope of Mount Locke at 6780 feet under shade of oak and pine trees on sandy loam.

In general, the species is widely distributed laterally and altitudinally, giving rise to diverse races described under seven varieties, now all in synonymy. This form from Davis Mountains falls in the *albispina* group.

These records from Trans-Pecos Texas mark the most southern known extent of *O. polyacantha;* perhaps the species is migrating south along the higher mountain chains.

SUMMARY

The area studied encompasses Jeff Davis, Presidio and Brewster counties, Texas, with the latter receiving most detailed consideration. Diversity of topography has produced a corresponding variety of habitats with at least thirty-five plant associations and many distinct populations of Opuntiae.

Distinguishing characteristics for species include growth habit, distance between areoles, form and color of spines, presence or absence of bristles, type of fruit, size of seed, and width of aril. Variations of characteristics within species are particularly expressed in number of spiniferous areoles on a joint, number of spines per areole, and length of individual spines. A key to the thirty-one species, varieties and hybrids found in the Big Bend Region precedes discussion of these entities.

Four new varieties are described: *O. imbricata* var. *argentea*, *O. lindheimeri* var. *chisosensis*, *O. macrocentra* var. *minor*, and *O. rufida* var. *tortiflora*. Each of these may be thought of as a potential source of new species. Three new hybrids are presented: *O. engelmannii* x *phaeacantha*, *O. grahamii* x *schottii* and *O. kleiniae* x *leptocaulis*. *O. spinosibacca*, the only known endemic species of Opuntia of the Big Bend Region, is newly described.

An example of disjunct distribution is found in *O. tunicata* which occurs here far from its closest recorded station in Saltillo, Coahuila. Its dwarf and typical forms suggest perpetuation of somatic differentiation in vegetatively reproduced clones.

REFERENCES

ANTHONY, M. S. 1949—An ecologic and systematic analysis of the genus Opuntia Miller in the Big Bend Region of Texas. Univ. Mich. doctoral thesis. (Microfilmed in June, 1951.)

——— 1954—Ecology of the Opuntiae in the Big Bend Region of Texas. Ecol. 35(3).

BENSON, L. 1940—The cacti of Arizona, Univ. of Ariz. Press, Tucson, Ariz.

BOISSEVAIN, C. H. AND C. DAVIDSON 1940—Colorado Cacti. Abbey Garden Press, Pasadena, Cal.

BRAVO, H. 1937—Las cactaceas de Mexico. Imprenta Universitaria, Mex.

BRITTON, N. L. AND J. N. ROSE 1919—The Cactaceae. Vol. I. Carn. Inst. Wash.

DENYES, H. A. 1951—Natural terrestrial communities of Brewster County, Texas, and adjoining areas, with special reference to the degree of restriction of certain small mammals to particular communities. Univ. Microfilms Pub. No. 2581. Doct. Dissert. Series. Ann Arbor, Mich.

ENGELMANN, G. 1849—Cacteae of plantae Fendlerianae Novi-Mexicanae Mem. Amer. Acad. Arts & Sci. 4(1):49-53.

——— 1856—Synopsis of the Cactaceae of the territory of the United States and adjacent regions. Proc. Amer. Acad. Arts & Sci. 3:259-311.

——— 1859—Cactaceae of the Boundary. Report of the United States and Mexican Boundary Survey II(1):3-78.

——— AND J. M. BIGELOW 1856—Description of the Cactaceae collected on route near the thirty-fifth parallel explored by Lt. A. W. Whipple in 1853, 1854. Rep. Explor. & Surv. for Rr. from Miss. River to Pacific Ocean. 3:27-58.

——— AND A. GRAY 1845—Plantae Lindheimerianae. Bost. J. Nat. Hist. 6:195-209.

GRIFFITHS, D. 1908—Illustrated studies in the genus Opuntia. I. Rep. Mo. Bot. Gard. 19:259-272. II Ibid. 20:81-97. III. Ibid. 21:165-174. IV. Ibid. 22:25-36.

HESTER, J. P. 1939—New species of cacti. Cactus & Succ. J. 10(10): 179-182.

MCDOUGALL, W. B. AND O. E. SPERRY 1951—Plants of Big Bend National Park. U. S. Govt. Print. Office, Wash., D. C.

OCHOTERNA, I. 1922—Las cactaceas de Mexico, Mexico, D. F.

SCHULZ, E. D. AND R. RUNYON 1930—Texas cacti. Proc. Tex. Acad. Sci. 14.

SPERRY, O. E. AND B. H. WARNOCK 1941—Plants of Brewster County, Texas. West Texas Hist. & Sci. Soc. Pub. 11:16-60.

TIDESTROM, I. AND SISTER T. KITTELL 1941—A flora of Arizona and New Mexico. Cath. Univ. Amer. Press, Wash., D. C.

PUBLICATIONS

ARNETT, Ross, H. Jr.—A Revision of the Nearctic Oedemeridae (Coleoptera) 1.00

BAILEY, V.—Cave Life of Kentucky 1.25

BUECHNER, H. K.—Life History, Ecology, and Range Use of the Pronghorn Antelope in Trans-Pecos Texas 1.00

CARPENTER, M. M.—Bibliography of Biographies of Entomologists 1.00

CHERMOCK, Ralph L.—A Generic Revision of the Limenitini of the World .50

COLE, A. C., Jr.—A Guide to the Ants of the Great Smoky Mountains National Park, Tennessee ..... .75

CONANT, Roger—The Reptiles of Ohio (second edition) 3.50

COOKE, W. B.—The Flora of Mount Shasta (and supplement) 1.00

FENDER, Kenneth M.—The Malthini of No. America (Coleptera-Cantharidae) 1.00

FISHER, Harvey I.—Adaptations and Comparative Anatomy of the Locomotor Apparatus of New World Vultures ..... .75

FITCH, Henry S.—Ecology of the California Ground Squirrel on Grazing Lands ..... .75

———Study of Snake Populations in Central California ..... .75

GOODRICH, C. & Henry van der Schalie—A Revision of the Mollusca of Indiana ..... .75

GREENE, E. L.—Manual of the Botany of the Region of San Francisco Bay, Cloth-bound 2.00
Unbound 1.50

———Flora Franciscana (Pt. 2 only) ..... .75

———Plantae Bakerianae 1.50

McGREGOR, E. A.—Mites of the Family Tetranychidae 1.25

MANTER, Harold W.—The Digenetic Trematodes of Marine Fishes of Tortugas, Florida ..... .75

MILLIRON, H. E.—Taxonomic & Biological Investigations in the Genus Megastigmus with Particular Reference to the Taxonomy of the Nearctic Species 1.00

MURLEY, Margaret R.—Seeds of the Cruciferae of Northeastern No. America 1.00

ORTON, Grace L.—Key to the Genera of Tadpoles in the U S. and Canada .25

POHL, Richard W.—A Taxonomic Study of the Grasses of Pennsylvania 1.00

RAFINESQUE, C. S.—Neogenyton ..... .25

———The Natural Family of Carexides ..... .50

———Scadiography of 100 Genera of Ombelliferous Plants, etc. 1.50

REED, Chas. A.—Locomotion and Appendicular Anatomy in Three Soricoid Insectivores 1.00

ROTH, Louis M.—A Study of Mosquito Behavior. An Experimental Laboratory Study of the Sexual Behavior of Aedes aegypti (Linnaeus) ..... .75

———A Study of Cockroach Behavior ..... .75

SEALANDER, John A., Jr.—Survival of Peromyscus in Relation to Environmental Temperature and Acclimation at High and Low Temperatures ..... .50

SCHEFFER & Slipp—The Whales & Dolphins of Washington State with a Key to the Cetaceans of the West Coast of No. America 1.00

SCHUSTER, R. M.—The Ecology and Distribution of Hepaticae in Central and Western New York, cloth-bound 2.50

———Notes on Nearctic Hepaticae III. A Conspectus of the Family Lophoziaceae with a Revision of the Genera and Subgenera 1.00

———Boreal Hepaticae. A Manual of the Liverworts of Minnesota and Adjacent Regions 4.00

SETTY, L. R. & K. W. Cooper—Studies in the Mecoptera 1.00

SINGER, Rolf—The Boletoideae of Fla. (TLe Boletineae of Fla. with notes on Extralimital Species III) 1.00

STEWART, R. E. et al—Seasonal Distribution of Bird Populations at the Patuxent Research Refuge 1.00

VARIOUS AUTHORS—Plant and Animal Communities 2.50

———Symposium on Paleobotanical Taxonomy 1.00